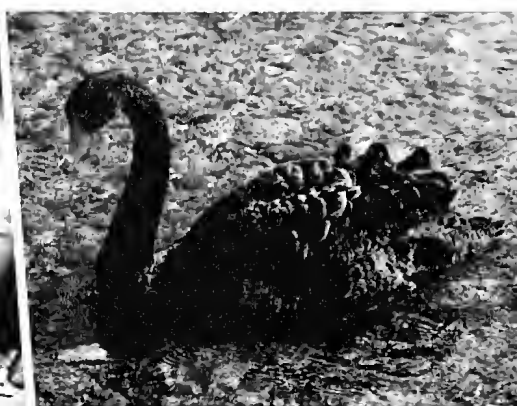
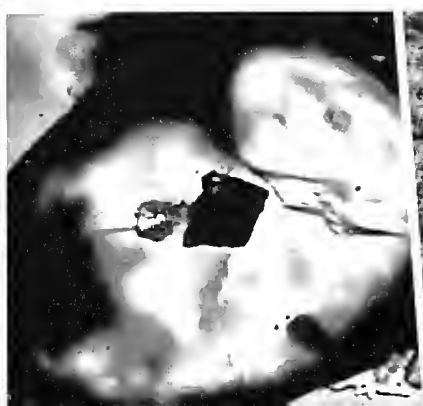
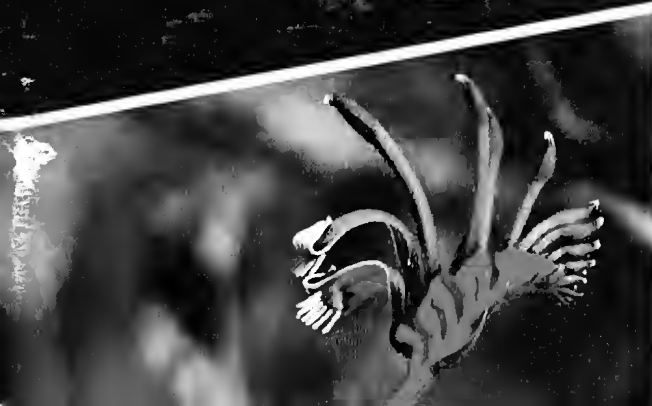




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Indian Ocean
Focus Issue

The Royal Society of Western Australia

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The Royal Society of Western Australia was founded in 1914. The Society promotes exchange among scientists from all fields in Western Australia through the publication of a journal, monthly meetings where interesting talks are presented by local or visiting scientists, and occasional symposia or excursions on topics of current importance. Members and guests are encouraged to attend meetings on the third Monday of every month (March–November) at 7 pm, Kings Park Board offices, Kings Park, West Perth, WA 6005, or as advertised, in the RSWA Proceedings, Diary of Events, or online.

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The *Journal of the Royal Society of Western Australia* was first published in 1914 and circulates widely within Australia and throughout the world. The journal has a large number of personal subscribers, many of whom are scientists working in Western Australia.

Cover design: The images symbolise the diversity of sciences embraced by the Royal Society of Western Australia. Counter-clockwise from the top they are: Wolfe Creek Meteorite Crater; the world-famous stromatolites at Shark Bay; the numbat (*Myrmecobius fasciatus*), Mangles' kangaroo paw (*Anigozanthos manglesii*) and Gogo fish (*Menamuraspis kaprios*), which are the faunal, floral and fossil emblems of Western Australia, respectively; a zircon grain (Western Australian rocks have yielded the oldest zircon dates in the world, up to 4.37 Ga); and the black swan (*Cygnus atratus*) that appears on the logos of the Royal Society and the coat of arms of the Government of Western Australia.



Indian Ocean
Focus Issue

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PREFACE

INDIAN OCEAN FOCUS ISSUE

The Pacific Ocean and its littoral has long provided a focus for scientific (and other) research. The Indian Ocean rather less so. The humanities have perhaps been less parsimonious in their attention to the Indian Ocean Basin – the Centre for Indian Ocean Peace Studies, a cooperative venture between Curtin University and the University of Western Australia flourished in the 1990s, sponsoring *The Indian Ocean Review* which was an important vehicle for the research on the history, geography, archaeology and politics of the region. Important publications of this era and genre included, Kenneth McPherson's *The Indian Ocean: a History of People and the Sea* (OUP, 1993) and *The Maritime Boundaries of the Indian Ocean*, by V L Forbes (Singapore University Press, 1995).

The Indian Ocean Marine Research Centre with two foci, Watermans Bay Marine Centre and in its new building on the UWA Campus, will boost marine science capacity in Australia.

It is important that the Royal Society of Western Australia acknowledges this significant theme: this issue includes papers on the Indian Ocean and its Western Australian littoral. It opens with a paper on Darwin's sojourn in the region, and is followed by papers on the biotas of Leeuwin Current off south-west Australia, and Fremantle Harbour.

The islands on Western Australia's Indian Ocean margin have an important ecological status, and an account of the recovery of seabird colonies on an island in the Houtman Abrolhos following the eradication of introduced predators provides an example of the efforts being made to conserve them. A companion paper on Dirk Hartog Island, the fieldwork for which was done in association with a cat eradication campaign, documents the food sources of the feral cats and the significance of these preferences for the ecology and conservation of the island.

Detailed accounts of some of the biotas of the Shark Bay and Jurien Bay areas fringing the ocean follow. A short research note on the ghost bat takes us inland to the Karijini National Park in the Pilbara.

The Society has traditionally encouraged young researchers, particularly through the annual postgraduate symposium. It is a pleasure to include extended abstracts from the 2014 symposium on the marine environments of the Kimberley, in the north of the state and Shoalwater Bay in the south-west.

Tsunami have had an important effect on the landforms, vegetation and human communities surrounding the Indian Ocean for millennia, and this is particularly the case in the Shark Bay region, where ancient tsunami carried massive blocks inland. This is one of the striking conclusions of a recent book on the geology of Shark Bay, reviewed in this issue.

A final short review considers two brief field guides to the freshwater fish of two regions of Western Australia's ocean margins.

P H Armstrong
Editor-in-Chief

Charles Darwin's Indian Ocean Experience

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Charles Darwin's time within the Pacific Basin is frequently described as a formative period in his development, while his traverse of the Indian Ocean in the first half of 1836 is much less emphasised. Yet his powers of observation remained at a high level in south-west Australia, on Cocos and Mauritius, at the Cape of Good Hope, and while at sea. 'The habit of comparison', as he called it himself, continued to be as important as ever. Themes noticeable in his earlier thinking and note-taking were consolidated during this period. He remained an avid collector of plant, animal and geological specimens and some of these specimens were to prove of appreciable significance.

KEYWORDS: Charles Darwin, Indian Ocean, HMS *Beagle*, comparison, islands, coral

INTRODUCTION

[T]he Pacific played a central role in shaping Darwin's experience of nature and the nature of modern science. ... As the Pacific shaped Darwin, so Darwin shaped the Pacific.

So wrote R MacLeod and P E Rehbock in the preface to *Evolutionary Theory and Natural History – Darwin's Laboratory* (1994). The role of the Pacific Basin in the development of Darwin's ideas – the Andes, the Galapagos and Tahiti in particular – has been abundantly stressed. In the decade or two after the *Beagle* voyage, the contributions of the naturalists that followed Darwin further enhanced the reputation of the Pacific as 'Laboratory'. Hooker, Wallace and Huxley, all of whom became close associates of Darwin, also had experience of Pacific environments.

Notable, too, in the development of the 'Pacific Laboratory', was J D Dana, geologist on the United States Exploring Expedition (1838–1842) under Lieut Charles Wilkes (Viola and Margolis, 1985). Dana's work on coral reefs was profoundly influenced by Darwin's accounts, and the two men corresponded about coral reefs, on barnacles, and on the nature of the deep valleys of the Great Dividing Range in New South Wales (Armstrong, 1993). This expedition spent some three years in the Pacific Ocean, but expended just over 30 days hurrying across the Indian Ocean, not pausing between the Straits of Sunda and the Cape of Good Hope. And although the *Erebus*, with Joseph Hooker aboard, briefly visited the islands of the southern Indian Ocean (Kerguelen, Crozet), many expeditions saw the Indian Ocean as a barrier to be hastily traversed on the way to, or from, where it was perceived the real work was done.

Darwin entered the Pacific Basin on 10 June 1834, and the *Beagle* stood out from Hobart Town, Van Diemen's Land (Tasmania) on 17 Feb 1836, a total of just over 19 months in the 'Pacific Laboratory'. In that time Darwin had explored the Andes, speculating about the nature of their uplift, and explored several island groups – the Galapagos, Tahiti and New Zealand. He had met indigenous people on the 'fine island' of Chiloé, off the

coast of Chile, as well as the Maoris, Polynesians and Australian Aborigines. He collected hundreds of specimens – rocks, plants, insects, shells and vertebrates. He wrote, on the traverse between Tahiti and Port Jackson (Sydney), the first draft of his theory of coral reefs and atolls: this was his first flirtation with the notion of gradualism. These were indeed all of consequence in the development of his ideas, but he had previously visited the Falklands, St Paul's, the Cape Verde Islands and Tierra del Fuego, as well as numerous sites on the eastern coast of South America, and on the homeward run HMS *Beagle* was to touch at the Atlantic Isles of St Helena, Ascension and the Azores. Almost all were important.

The purpose of this article is to emphasise the significance of the traverse of the Indian Ocean to Darwin's thinking. This is taken as the period between the *Beagle's* entering Princess Royal Harbour, Western Australia (6 March 1836) and her departure from Cape Town on 18 June, both dates exclusive, a total of just 100 days; a short period compared with the Pacific sojourn, but over three times as long as USS *Vincennes* on the US Exploring Expedition. It thus includes his explorations of the 'continental' environments around King George's Sound in south-west Australia and at the Cape of Good Hope, as well as visits to the Cocos (Keeling) Islands and Mauritius (which Darwin sometimes refers to as the Isle de France). Just under half of this time was on land, or at anchor close to land.

Table 1. Time spent on land and at sea during HMS *Beagle's* Indian Ocean Traverse.

Locality	Dates (1836)	Total Days
King George's Sound	7–14 March	7
King George's Sound to Cocos	15 March – 1 April	18
Cocos	2–11 April	10
Cocos to Mauritius	12–29 April	17
Mauritius	30 April – 9 May	10
Mauritius to Cape	10–31 May	21
Cape of Good Hope	1–17 June	17
Total		100

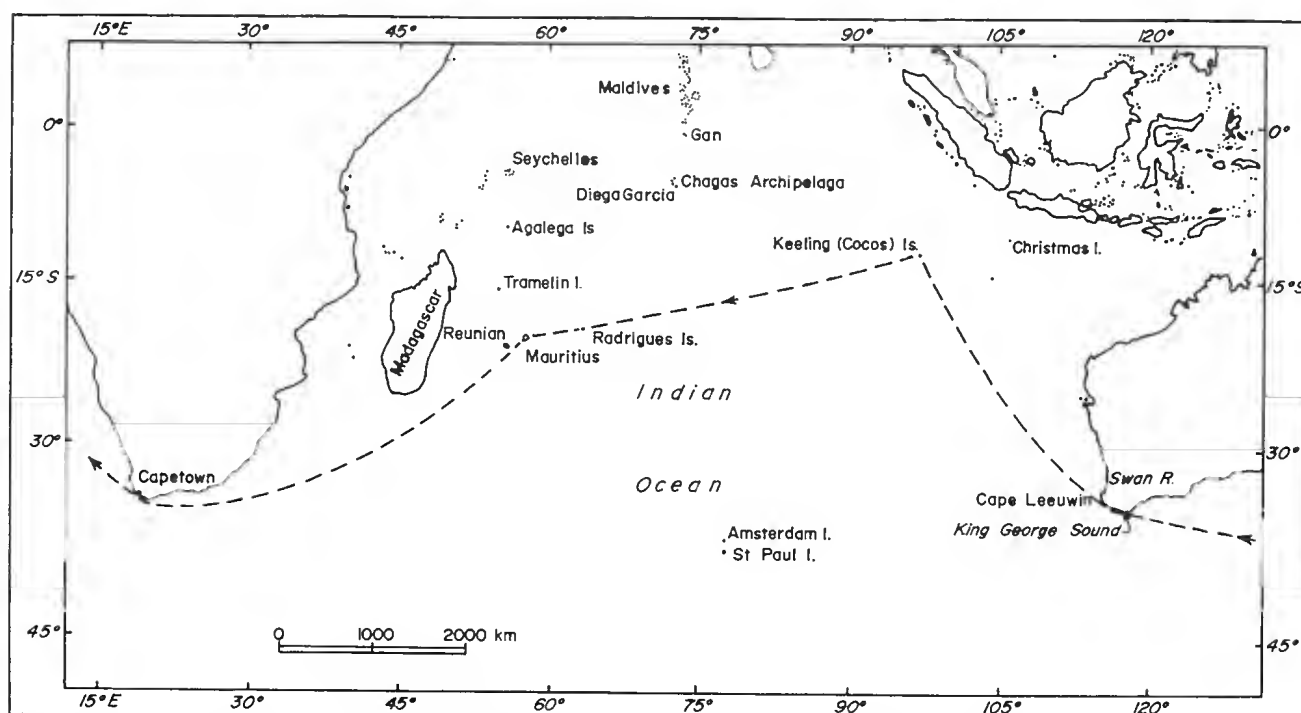


Figure 1. Route of HMS *Beagle* across the Indian Ocean.

THE INDIAN OCEAN EXPERIENCE

Powers of Observation, an Eye for Detail and the 'Habit of Comparison'

Darwin did not like the sea, and was frequently sea-sick; indeed at one time considered abandoning the voyage. It would not be surprising if Darwin was feeling wearied towards the end of the voyage, and there is some evidence that he collected specimens less assiduously than earlier. But his eye for detail was as good as ever. Moreover, it can be seen that he was arranging some of his material around conceptual frameworks that were to be of importance to him later.

When the ship was 50 miles (80 km) west of Cape Leeuwin, on 18 March 1836, he describes what he called *Confervae* – filamentous algae or phytoplankton. His account provides a good example of the level of detail typical of his notes (Figure 2). He:

...observed the sea, covered with fine particles, as if thinly scattered with fine dust. Some water being placed in a glass, with an ordinary lens, the particles appeared like equal sized fibres of any white wood. On examination under higher powers, each particle is seen to consist of from 10–15 cylindrical fibres. These are loosely attached side by side all together; their extremities are seldom quite equal, a few projecting at each end. The bundle was about 1/50th of [an] inch, but any separate fibres rather less, perhaps 1/60th. The color a very pale brownish green. Each separate fibre is perfectly cylindrical & rounded off at both extremities (Cambridge University Library Darwin Archive [CULDA] 31.2/349)

During the voyage Darwin was constantly comparing the observations in one locality with those he made

elsewhere. It was this comparative approach that was in no small measure the key to his success. He did this frequently in his traverse of the Indian Ocean. On the back of the above note he wrote:

On passage from Mauritius to C of Good Hope Lat 37° 30'. Sea with the green flocculent tufts & [illeg] dust, during a calm day in very great quantities. Must be a most abundant marine production.

Here is his account of the robber crab (*Birgus latro*) (Figure 3) on the Cocos (Keeling) Islands:

These monstrous crabs inhabit in numbers the low strips of dry coral land; they live entirely on the fruit of the cocoa nut tree. Mr Liesk informs me he has often seen them tearing, fibre by fibre, with their strong forceps, the husks of the nut. This process they always perform at the extremity, where their three eyes are situated. By constant hammering the shell in that soft part is broken & then by the aid of their narrow posterior pincers the food is extracted I think this is as curious a piece of adaptation and instinct as I ever heard of. The crabs are diurnal in their habits; they live in burrows which frequently lie at the foot of the trees. Within the cavity they collect a pile, sometimes as much as a large bag full of the picked fibre & on this they rest. At night they are said to travel to the sea where the young are hatched, and during the early part of their life they remain. ... Their flesh is very good food. ... They are exceedingly strong. The back is coloured dull brick red: the under side of the body & legs is blue, but the upper side of the legs clouded in dull red. In the 'Voyage par un Officier du Roi' to the Isle of France there is an account of a crab that lives on Cocoa nuts in a

1836. 377 *Coast of Australia* 244

Confervae March 18th The ship being about 50 miles from Cape Leeuwin, observed the sea covered with particles, as if things scattered over with fine dust. - Some water being placed in a paper with an oblong lens, the particles appeared like small bits of the fibres of very white wood. - On examination under higher powers each particle is seen to consist of from 1-16 of cylindrical fibres. These are loosely attached side of side all together; their extremities are seldom quite equal, a few projecting at each end. - The bundle was about $\frac{1}{50}$ of an inch in length, but ^{an average} each fibre rather less perhaps $\frac{1}{100}$. - The color a very pale brownish green. - Each bundle of fibres is perfectly cylindrical & composed of a ^{small number} of cylindrical fibres, the whole is divided ^{into} 3000 transverse partitions, which occur at regular intervals, being about half the diameter of the fibres. ^{Between} each bundle is contained, but by microscope does not suffice for 10. - Extremities cylindrical with little or no granular matter. - The bundles meet & stick, & are enveloped in some adhesive matter, becoming a glaze on touching the sides they almost always adhere. - The ^{entire} quantity of sea covered with Confervae was not very extensive. - The morning calm. - Tide similar account near 5. 1836.

Figure 2. Charles Darwin's notes on Confervae, 50 miles (80km) off Cape Leeuwin, Western Australia, 18 March 1836 (the year at the head, 1835, is of course an error). Cambridge University Library.

small island North of Madagascar: probably it is the same animal ...

Mr Liesk informs me that the crabs with swimming plates to posterior claw employ this tool in excavating burrows in fine sand and mud & he has repeatedly watched the process. (CULDA 31.362)

Here is Darwin the observer at his best. He describes the organism accurately; most of his observations have been confirmed in modern studies (eg Drew, *et al*, 2010). He enlivens his account with information from the observations of a resident of the islands, and material from a book to which he had access aboard the *Beagle*, but clearly separates his own observations from those of others. He gives as much attention, or more, to the behaviour of the creature as to its appearance: feeding and burrowing are described in detail, along with the lining of burrows with fibre. Breeding and daily rhythms are mentioned. The organism is related to its habitat – coconut palm groves, growing in sandy soil adjacent to the beach. The account strikingly integrates the animal's morphology with its habitat and behaviour. There are signs of the comparative approach that was so fundamental to Darwin's work. He refers to 'adaptation',

a key component of his evolutionary thinking, and 'instinct' presaging his works on animal behaviour, such as *The Expression of the Emotions in Man and Animals* (1872).

In both southwest Australia and in Africa Darwin made extremely detailed geological observations. His first impression of King George's Sound was of the 'bare smooth conical hills' similar to those he had encountered in South America; he continued 'I at once suspected that the observation of Humboldt of the frequency of the form in hills of gneiss-granite, would be verified in this part of Australia.' (Darwin had been reading Alexander von Humboldt's *Personal Narrative* of his journey to South America throughout the voyage, and was profoundly influenced by it. Ref: CULDA 38.864-5). His descriptions of the granites and granite landforms of the Cape were just as detailed:

The granite is coarse-grained & contains very large crystals of feldspar; it is in many parts traversed by veins; ... it contains balls of a dark color which consist of an aggregation of minute scales of black mica. (CULDA 38.902)

Darwin was one of the first to identify the origin of that characteristic African landform the *kopje* –



Figure 3. Coconut or robber crab, from *Dictionnaire D'Histoire Naturelle*, 1849.

appreciating that they were similar to the forms occurring in Australia. The massive rounded boulders formed through the decomposition of granite, and the spheroidal weathering of the resulting corestones.

The granite is subject to extreme decomposition, & hence, when protected is covered by a great thickness of rock, reduced into the state of soil. At the village of Paarl there are some extraordinary fine examples of loose balls of enormous size lying on the summits of the base mammiform hills of granite. Parallel & vertical fissures cross the mountains in directions at right angles to each other. These may now be seen of various widths, & it would appear that the great balls are only the remnants of original cubical masses. Besides the general description circumscribed patches of the granite yield to the weather, much more readily than the adjoining parts. As we see in some granites spherical masses projecting outwards from processing a harder & slightly different structure, so here cavities exist on the sides of steep rocks section; From the thinness of the overhanging lip, or front it appears certain, that no other cause than the quiet action of the weather has removed the central parts. A very large hollow, forming a cave, exists in the lower surface of one of the great balls on the Paarl. — This globular mass is perhaps about 30 ft high, it rests on several points, within which is a smooth arched cave, frequented by cattle. On the sides of

some steep masses, the granite is worn away, into extensive shallow cavities of irregular forms, which resemble the defective parts, of any mass of cast metal. (CULDA 38. 902-4)

This detailed study of weathering processes shows that Darwin clearly understood the long periods over which geological processes operate. He was by this time fully cognisant with Charles Lyell's doctrines of uniformitarianism, set out in *Principles of Geology* (1830–1833), which he had in his possession. And it is clear from his notes that Darwin compared his geological observations of King George's Sound with his impressions of the rocks and landforms of the Cape of Good Hope and was able thereby to generalise about the processes in operation.

Human Communities and the Cultural Landscape

Yet it was not just in his geological and biological enquiries that reveal Darwin as both a first rate observer and one with the ability to integrate and see the 'big picture'. He had little knowledge of anthropology – and indeed this science was not well developed. Nevertheless he was curious about the human communities with which he came into contact often making extensive notes about their customs and traditions. Darwin's detailed description of an Aboriginal corroboree at King George's Sound was given in a previous issue of this journal (Armstrong, 2009). On Cocos he witnessed what seems to have been a funeral ritual, and he describes the manner in which the Malay people caught turtles and fish.

In Mauritius and South Africa he was curious about the many races of humankind he encountered and the way in which they got along together – he had some astringent criticisms of British colonial policy. 'Cape Town is a great inn' he wrote in a letter to his sister (CULDA 97 [ser.2]:32-3) and Burkhardt and Smith, 1985, 493) The Europeans were English, Dutch and French, with 'scattered people from other parts'. There were Malays in significant numbers, but 'the number of negroes is not very great.' He deplored the manner in which the Bushmen were 'the ill-treated aboriginals of the country'. His diary entry for 30 April 1836 says of Mauritius: 'One of the most interesting spectacles in Port Louis is the number of men of various races'. The Indians, he noted, were 'noble looking' and 'imposing'. He seems sympathetic to the 'poor man' who was 'a confirmed opium eater, of which fact his emaciated body & strange drowsy expression bore witness.' The influence of his Edinburgh medical training is perhaps apparent here both in his sympathetic approach and appreciation of symptoms. He also deplored the manner in which the Malay people on Cocos were held in a type of serfdom. Bigot he was not.

In Mauritius, at the Cape of Good Hope and in Cocos he composed almost lyrical descriptions of landscapes and the manner in which the human community interacted with them. Here are his first impressions of Mauritius, seen from the deck of the *Beagle*, 29 April 1836:

The sloping plain of the Pamplemousses, scattered over with houses & coloured bright green from the large fields of sugar cane, composed the foreground. The brilliancy of the green was the more remarkable because it was a colour which

generally is only conspicuous from a very short distance. Towards the centre of the island groups of wooded hills arose out of the highly cultivated plain, their summits, as so commonly happens with ancient volcanic rocks, being jagged by the sharpest points. Masses of white clouds were collected around these pinnacles, as if merely for the sake of pleasing the stranger's eye. (*Diary*)

Coral Reefs and Atolls

The genesis of Darwin's 'Coral Atoll Theory' lies firmly in the Pacific. Correspondence with a Mr R E Alison, in June 1835, while he was still in South America, suggests that Darwin was speculating on the possibility of the 'sinking of land' in the 'Pacific islands', compensating perhaps for an uplift or a rising on the Pacific coast of South America (CULCA 36.1: 427 and Burkhardt and Smith, 1985, 450). On the *Beagle's* voyage westwards across the Pacific, he seems to have climbed aloft, and looked down onto the lagoons of atolls from quite close at hand:

... from the Mast-head it was possible to see at Noon Island across the smooth lagoon to the opposite side. The great lake of water was about 10 miles wide. (*Diary*, 13 November 1834)

At Tahiti (15–26 November 1835) he made a careful study of the relationship of the coral reefs to the main shoreline both for the islet of Eimeo (now Moorea) and for Tahiti itself. He also looked at the detailed ecology of the reefs and their microtopography, noticing that coral growth was most vigorous on the outer, wave-splashed edge of the reef. He appreciated that coral would only grow within '25 to 35 fathoms' of the surface (approx 40–65m), and noted how steeply the sea floor sloped away a relatively short distance from the shore. A few days later, the ship passed, but did not land on, the archipelago of Aitutaki (Darwin and his captain, FitzRoy refer variously in their writings to Whytooacke, Whylootake, or Waiutaki), which represented...

A union of two prevailing types of structure... A hilly irregular mass was defined by a well defined circle of reefs, which in great part have been converted to narrow strips of land, which [Captain James] Cook calls them half-drowned.... (*Diary*, 3 December 1835) ..

This appears to be Darwin's first written indication of an appreciation of a link between atoll formation and 'drowning': it is interesting that there is a link with Captain Cook.

It was probably shortly after this, but before his arrival in New Zealand on 21 December 1835, that Darwin penned his 23-page memorandum entitled 'Coral Islands' (CULDA 40/5). Here we see the first coherent expression of his notion that fringing reefs (where the coral reefs are attached to the shore), barrier reefs (where the island is separated from the reef by a moat-like lagoon) and atolls (Darwin often used the term 'lagoon islands') are members of a continuous series, one form progressing into another through subsidence (or drowning).

Darwin therefore developed his Coral Atoll Theory long before he actually had his feet on a real atoll!

In his *Diary* entry for 12 April 1836, written shortly after the *Beagle* had departed from the Cocos (Keeling) islands in the eastern Indian Ocean, Charles Darwin wrote:

I am glad we have visited these Islands; such formations surely rank high amongst the most wonderful objects of the world. It is not a wonder that first strikes the eye of the body, but rather after reflection the eye of reason.

There is a certain triumphalism in this: Darwin seems to be appreciating his own 'eye of reason'. It was at Cocos that the Coral Atoll Theory 'came together'. He was able to apply what had hitherto been largely a theoretical construct to a real world example of an atoll or 'lagoon island' (Figure 4). He wrote extremely detailed notes, both on the geomorphology of the coral reefs and the



Figure 4. Inner lagoon, Cocos (Keeling) Islands.

islands, and on the ecology of the corals themselves. He drew neat cross sections across the reefs, islands and lagoon (CULDA 41). The officers of the *Beagle* conducted an offshore survey and it was noted that the seabed sloped away very steeply from the island shore. No bottom was found some 2200 yards (approx 2 km) from the breaking waves, with a line some 7200 feet in length..

In his *Diary* entry for 12 April, the day of the ship's departure from Cocos, Darwin summarised his ideas as follows – much more succinctly than in the earlier manuscript:

... we must consider this island as the summit of a lofty mountain. ... If the opinion that the rock-making Polypi continue to build upwards as the foundation of the Isd from volcanic agency, after intervals, gradually subsides, is granted to be true, then probably the Coral limestone must be of great thickness. We see certain Isds in the Pacific, such as Tahiti and Eimeo ... which are encircled by a Coral reef separated from the shore by channels & and basins of still water. Various causes tend to check the growth of the most efficient types of Corals in these situations. Hence, if we imagine such an Island, after long successive intervals to subside a few feet, in a manner similar but with a movement opposite to the continent of S. America, the coral would continue upwards, rising from the foundation of the encircling reef. In time the central land would sink beneath the level of the sea & disappear, but the coral would have completed its circular wall. Should we not then have a Lagoon Island? Under this view, we must look at a Lagoon Isd as a monument raised by myriads of tiny architects, to mark the spot where a former land lies buried in the depths of the ocean.

All this material was combined into the elegant, very thorough case-study of the Cocos Islands that comprises the opening chapter of *The Structure and Distribution of Coral Reefs* (1842), first volume of *The Geology of the Voyage of the Beagle*. The fact that he commenced the work with this case-study implies that he considered his sojourn on Cocos as providing an important key to his study of coral reefs and atolls.

Darwin continued his work on coral at Mauritius, some three weeks later.

On the NW, W & SW of the islands coral rock such as [is] now forming the reefs is commonly found above the reach of the very highest tides ... To the northward of Port Louis the surface of the country to a height of 30 or 40ft, & to a considerable distance inland is coated by a bed of partially cemented fragments of stony branching corals ... the rock is composed of precisely the same materials such as are lying on the beach. ...

The elevation above the mean level of the sea appears considerable to exceed that of the reefs in the Pacific; hence I suspect it is owing to the rising of the land which has affected the whole Island. (CULDA 38.885-898)

Darwin was able to compare the topography and ecology of reefs in the Pacific, and at Cocos – where he

felt certain that generally the land had fallen relative to the sea – with the situation on Mauritius where he had strong evidence that the opposite was the case. In his book of *Coral Reefs* he provides a map showing those areas where he felt that submergence had occurred and those dominated by emergence. Had the experience of the Pacific Laboratory not been supplemented by studies of the two islands in the Indian Ocean Darwin's work on coral reefs would have had major lacunae, and his first experimentation with the notion of gradual change in the environment less successful. We may note in passing that in his investigation of reefs he not only emphasises Lyellian gradual change, but the idea of a dialogue between organisms (the coral polyps) and their environment: a notion fundamental to his later work.

Island Biotas and Long Distance Dispersal

Darwin recognised the depauperate nature of island biota at a number of the islands and archipelagoes he visited during the voyage. On Cocos he describes the 'vigorous' vegetation – a response to the tropical climate. But he noted:

Besides the Cocoa nut which is so numerous as to first appear the only tree, there are five or six other kinds. One called the Cabbage tree grows in great bulk in proportion to its height & has an irregular figure ... Besides these trees the number of native plants is exceedingly limited: I suppose it does not exceed a dozen. (*Diary* 2 April 1836)

The 'Cabbage tree' was *Scaevola sericea* (*Scaevola Koenigii* in John Henslow's account of the Cocos collection of plants – Henslow was Darwin's friend and botany teacher at Cambridge). It remains one of the most conspicuous plants on the archipelago, forming a loose shrubby barrier along the shores. Darwin's count of the plant species diversity was an underestimate, but he was right in principle: in comparison with the biota of the forests of South America, or even Australia, it was poor. It was the same for animals. 'There are no true land birds' he said, 'a snipe and a land rail' being the only waders, all other species present being 'birds of the sea'. The 'snipe' was probably the ruddy turnstone (*Arenaria interpres*), the land rail a unique subspecies of the buff-banded rail (*Rallus [Gallirallus] philippensis andrewsi*), now only found on the tiny atoll of North Keeling, which HMS *Beagle* briefly surveyed on 12 April 1836, but no landing was made, Darwin simply noting: 'This likewise is a small Lagoon Isd, but its centre is nearly filled up.'

He continued:

Insects are very few in number: I must except some spiders & a small ant which swarms in countless numbers at every spot & place. (*Diary*, 2 April 1836)

Significantly Darwin again clearly distinguished between the number of species, from the number of individuals. A small note kept with Darwin's zoological annotations lists 12 species, including flies, ants, a couple of species of moths and a beetle. When writing the visit up for *The Voyage of the Beagle* he amends the total to 13. He notes also a single species of lizard. In his writings on the plants and animals of the Cocos (Keeling) archipelago words such as 'paucity', 'scanty', 'few' and 'only' occur.

Not only did he appreciate the low biodiversity of the island, there is evidence that he gave at least some thought to the possible means of dispersal of organisms to the islands. Darwin handed over the plant specimens he collected at Cocos to Professor Henslow and, in 1838, they were described in an article in *Annals of Natural History*. In this paper Henslow wrote: 'Mr Darwin heard of the trunks of trees, and of old cocoa-nuts being washed on the shore'. Darwin could hardly have missed finding seeds and other organic debris along the tide-line of Horsburgh, Direction and Home Islands, all of which he visited. He drew attention in his *Diary* to the abundance of seabirds, although he did not, at the time seem to have speculated that these might have been dispersal vehicles, although he paid considerable attention to this point later. Nevertheless in editing his diary for publication as *The Voyage*, he wrote that the archipelago 'had quite the character of a refuge for the destitute'. This implies both the idea of the paucity in the biota in terms of species numbers, and the idea of a long and difficult journey for those that eventually became successfully established. He continued:

As the islands consist entirely of coral must at one time have existed as mere water-washed reefs, all their productions must have been transported here by the waves of the sea.

These words, however were written after his 'conversion' to an evolutionary outlook in the (northern) spring of 1837. By then he appreciated the importance of the link between long-distance dispersal and evolution: if all life on earth had a common origin, or was ultimately derived from a few simple forms, the biotas of remote islands must have been derived from elsewhere.

There are a couple of other observations that may have brought the subject of long distance dispersal into his mind while at Cocos. In his annotations on coral he noted the presence of 'small pumice pebbles on beach from Sumatra, like the seeds'. Lumps of vesicle-filled volcanic material are frequently found on the shores, having floated there from volcanic eruptions in Indonesia (I myself found several on the shore of Home Island).

Further he records collecting 'A piece of a well rounded boulder of compact greenstone [dolerite] found in the coral breccia of the Northern Isd: in possession of Capt. Ross'. Captain Ross, the proprietor of the islands, was away at the time of Darwin's visit, so the fragment of rock must have been handed over by Mrs Ross or Mr Liesk. In *The Voyage* the original boulder is described as being 'rather larger than a man's head' and on the basis of comparison with descriptions of similar phenomena mentioned by other authors the suggestion was offered that it had arrived on the lonely islet of North Keeling amongst the roots of a far-travelled tree. Again evidence – as he saw it – for the reality of long distance dispersal.

Despite his detailed geological notes, Darwin's observations on the plants and animals of Mauritius are less rigorous. He admits in his notes that his attention wandered; he wrote: 'since leaving England I have not spent so idle and dissipated a time'. He collected few specimens, apart from a very few insects and a frog.

This last was in due course identified and depicted in volume 5 of *The Zoology of the Voyage of the Beagle* (Thomas Bell, 1843) as *Rana mascariensis* (now known as

Ptychadena mascareniensis: the Mascarene grass frog or Mascarene ridged frog). Darwin found 'this pretty species ... on swamps near the sea'; always interested in animal behaviour and locomotion he commented on 'the extraordinary height of its leaps.' Although Darwin cannot have known much of its distribution when he collected it, Bell noted that it had 'also been found in the Seychelles, Madagascar and the Island of Bourbon [Réunion]'. Darwin seems to have deduced from this that it had been introduced: recent studies, including DNA testing confirm that he was right (Staub, 1993, Vences, Kosuch *et al* 2004). In *Natural Selection*, the massive 'big species book', written 1856–1858, but unpublished until 1975, of which *On the Origin of Species* was a 'digest' he declaimed:

It would be superfluous to give the cases amongst my notes of the enormous increase of Birds, fish, frogs, snails & insects, when turned out into new countries: the one island of Mauritius would afford striking instances of all these classes except fishes. (Chapter 5)

He used the frog example in *On the Origin*, but with a slight twist.

The general absence of frogs, toads and newts on so many oceanic islands cannot be accounted for by their physical conditions; indeed it seems that islands are particularly well fitted to these animals; for frogs have been introduced into Madeira the Azores and Mauritius, and have multiplied so as to become a nuisance. (Chapter '12)

Darwin pointed out that these animals and their spawn are soon destroyed by sea water, so their transport by sea would be rare. Evolutionary theory, emphasising that life begets life and that living things can only reach remote islands by long distance dispersal, explains their absence. 'But why, on the theory of creation, they should not have been created there, would be very difficult to explain.'

CONCLUSIONS

Charles Darwin spent three and a half months within the Indian Ocean Basin. His powers of observation of plants, animals, marine organisms, rocks, landforms and human communities remained at a high level. As he did earlier in the voyage, he frequently used the comparative method. His traverse allowed him to confirm ideas that he had generated elsewhere, such as the Coral Atoll Theory, applying it to Cocos, and slightly modifying it to take account of the evidence of rising land levels he noticed in Mauritius. He compared the rounded granite topography of King George's Sound with the *kopje* landforms around Paarl at the Cape, thus entrenching the Lyellian views of gradual change ever more firmly in his mind. He had already commented on the relatively low species diversity of island groups such as St Paul's in the Atlantic and Tahiti in the Pacific. His observations on Cocos, and perhaps to a lesser extent Mauritius confirmed this notion; there also seem to have been early stirrings of the idea of long distance dispersal. He did not link the ideas of low diversity, evolution and dispersal until later, but the foundations were

established. He captured a frog on Mauritius, only later understanding its significance.

The Pacific was of course significant to his development, but not all-important. The Indian Ocean experience can be seen as an early stage the of the thoughtful process that continued in the two years following his return to England that led to his insight into natural selection.

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REFERENCES

- ARMSTRONG P H 1993. The contrasting views on the Australian valleys of Charles Darwin and James Dwight Dana: an early problem in Australian geology. *Journal of Australian Studies* 39, 53–64.
- ARMSTRONG P H 2009. Charles Darwin in Australia. *Journal of the Royal Society of Western Australia, Special Issue on Darwin and Evolution* 92, 385–388.
- BARLOW N (ed) 1933. *Charles Darwin's Diary of the Voyage of HMS Beagle*. Cambridge University Press, Cambridge.
- BELL T 1843. *The Zoology of the Voyage of HMS Beagle, volume 5 Reptiles [and Amphibia]*. Colburn, London.
- BURKHARDT F & SMITH S 1985. *The Correspondence of Charles Darwin*, volume 1 (1821–1836). Cambridge University Press, Cambridge.
- DREW M M, HARZSCH S, STENSMYR M, ERLAND S & HANSSON B S 2010. A review of the biology and ecology of the Robber Crab, *Birgus latro* (Linnaeus, 1767) (Anomura: Coenobitidae). *Zoologischer Anzeiger*, 249, 45–67.
- DARWIN C R 1842. *The structure and distribution of coral reefs. Being the first part of the geology of the voyage of the Beagle, under the command of Capt. Fitzroy, RN during the years 1832 to 1836*. Smith Elder and Co, London.
- DARWIN C R 1859. *On the Origin of Species by means of natural selection, or the preservation of favoured races in the struggle for life*. Murray, London.
- DARWIN C R 1860. *Journal of researches into the natural history and geology of the countries visited during the voyage of HMS Beagle round the world*. Murray, London. This work is almost universally referred to as *The Voyage of the Beagle*.
- HENSLOW J S 1838. Florula Keelingensis: an account of the native plants of the Keeling Islands, *Annals of Natural History*, 1, 337–347.
- MACLEOD R & REHBOCK P E (eds) 1994. *Evolutionary Theory and Natural History – Darwin's Laboratory*, University of Hawai'i Press, Honolulu, ix–x.
- VENCES V, KOSSUTH J, RÖDEL M, LÖTTERS S, CHANNING A, GLAW, F & BOHME W 2004. Phylogeography of *Ptychadena mascareniensis* suggests transoceanic dispersal in a widespread African-Malagasy frog lineage. *Journal of Biogeography*, 31(4), 593–601.
- VIOLA H J & MARGOLIS C (eds) 1985. *Magnificent Voyagers: the US Exploring Expedition, 1838–1842*. Smithsonian Institution Press, Washington DC.
- VON HUMBOLDT A 1814. *Personal narrative of travels to the equinoctial regions of the New continent, during the years 1799–1804*. Translated by Williams H M, Longman, Hurst, Rees, Orme and Brown, London.
- STAUB F 1993. *Fauna of Mauritius and associated flora*. Précigraph Ltd., Mauritius.
- STAUFFER R C (ed) 1975. *Charles Darwin's Natural Selection, being the Second Part of His Big Species Book, Written from 1856 to 1858*. Cambridge University Press, Cambridge.

Bibliographic Note. Nora Barlow's 1933 transcription of Darwin's Beagle *Diary* was used – this is the most widely available version, although there are others. I used a recent reprint of the first edition of *On the Origin*. Similarly I used a modern reprint of the 1860 edition (almost identical to the 1845 printing, but with significant differences from the 1839 version) of *The Voyage* (ie *Journal of Researches*). Although I inspected some of Darwin's original field notes in Cambridge, many of these are now available in Darwin Online (<http://darwin-online.org.uk>), and I checked my own transcriptions against these.

Euphausiid assemblages in and around a developing anticyclonic Leeuwin Current eddy in the south-east Indian Ocean

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The composition, distribution and abundance of euphausiids in and around an anticyclonic eddy of the Leeuwin Current were investigated in the south-east Indian Ocean off Western Australia (31°–34°S). In total, 22 euphausiid species were identified, two of which, *Euphausia sanzoi* and *Thysanopoda astylata*, are new records for the south-east Indian Ocean. In addition, five species represent new records for Australian EEZ waters and seven are new records for the latitude of the eddy field. *Euphausia recurva* and *Stylocheiron carinatum* were the most abundant species in the Leeuwin Current and eddy perimeter, reaching mean abundances of $135.5 \pm 22.3 \text{ m}^{-2}$ and $70.5 \pm 12.2 \text{ m}^{-2}$, respectively. *Pseudeuphausia latifrons* was the most abundant species over the shelf ($52.1 \pm 14.0 \text{ m}^{-2}$). Species richness was greater in the eddy and surrounding oceanic waters (18–20 species) than on the adjacent shelf (11 species). Of the water column properties included in a multivariate multiple regression analysis, only depth made a significant contribution to explaining the variation in euphausiid assemblages, probably due to mixing of water masses in the developing eddy. This study has revealed the influence of mixing processes associated with a Leeuwin Current eddy on holoplanktonic euphausiids in the south-east Indian Ocean.

KEYWORDS: Euphausiacea, warm core eddy, boundary current, entrainment, new records

INTRODUCTION

Despite the importance of euphausiids (krill) in marine food webs, there have been no studies dedicated to describing the distribution and abundance of euphausiid species within the Leeuwin Current system of the south-east Indian Ocean. During earlier plankton investigations further offshore of the Leeuwin Current system during the International Indian Ocean Expedition, 32 euphausiid species were recorded in oceanic waters along the 110°E meridian (9°–32°S) (McWilliam 1977). To the north of Western Australia, 12 euphausiid species, including *Euphausia recurva* Hansen 1905 and *Pseudeuphausia latifrons* (Sars 1883), have been recorded in the head waters of the Leeuwin Current (Taniguchi 1974; Wilson *et al.* 2003). Within the Australian Exclusive Economic Zone, eight euphausiid species are expected to occur off south-western Australia between 31° and 34°S (Davie 2002).

The Leeuwin Current is an anomalous, poleward flowing, eastern boundary current off the coast of Western Australia (Cresswell & Golding 1980; Ridgway & Condie 2004; Waite *et al.* 2007a). Like other boundary currents, it has an important influence upon longshore and cross-shelf variability and transport of planktonic biota and is responsible for southward (temperate) range extensions of tropical species (Maxwell & Cresswell 1981; Hutchins and Pearce 1994; Fox & Beckley 2005; Pearce *et al.* 2011). The Leeuwin Current is increasingly energetic and variable along its southwards trajectory and the formation of meso-scale perturbations such as meanders and anticyclonic eddies enhance shelf-ocean exchange (Weller *et al.* 2011; Holliday *et al.* 2012). Such meso-scale features are more frequent during the austral autumn and winter months when the Leeuwin Current is strongest and opposing southerly winds are weak (Feng

et al. 2003). These features drive the cross-shelf variability of planktonic biota and there are important latitudinal differences in the dispersal or retention of shelf waters that correspond with regions of recurrent meso-scale instability (Feng *et al.* 2010; Holliday *et al.* 2012).

Detailed *in situ* investigations of a developing anticyclonic eddy of the Leeuwin Current and surrounding waters (Paterson *et al.* 2008; Holliday *et al.* 2011) provided the context to examine the euphausiid assemblages off south-western Australia in the late austral autumn. This particular eddy was defined as a mix of Leeuwin Current, oceanic, and shelf waters and its constituent ichthyoplankton assemblage reflected the different source waters (Paterson *et al.* 2008; Holliday *et al.* 2011). The aim of this study was to document the euphausiid assemblage within an eddy of the Leeuwin Current system in the south-eastern Indian Ocean.

METHODS

Sampling

This study is based upon intensive oceanographic (Paterson *et al.* 2008) and biological (Holliday *et al.* 2011) sampling of a developing anticyclonic eddy and surrounding waters off the coast of south-western Australia (31°–34°S; up to 200 nm offshore) over the period 2–28 May 2006. The developing eddy was identified through sequential satellite observations of sea surface temperature and sea surface height anomaly (Fig. 1). A meander was initially formed which developed into the anticyclonic eddy, continuing to circulate after the 26 day sampling period during May 2006. The eddy then broke away and, by mid-August, had drifted further westward. Altimetry and satellite images of sea-surface temperature were sourced from the Integrated Marine Observing System (IMOS) website (www.oceancurrent.imos.org.au).

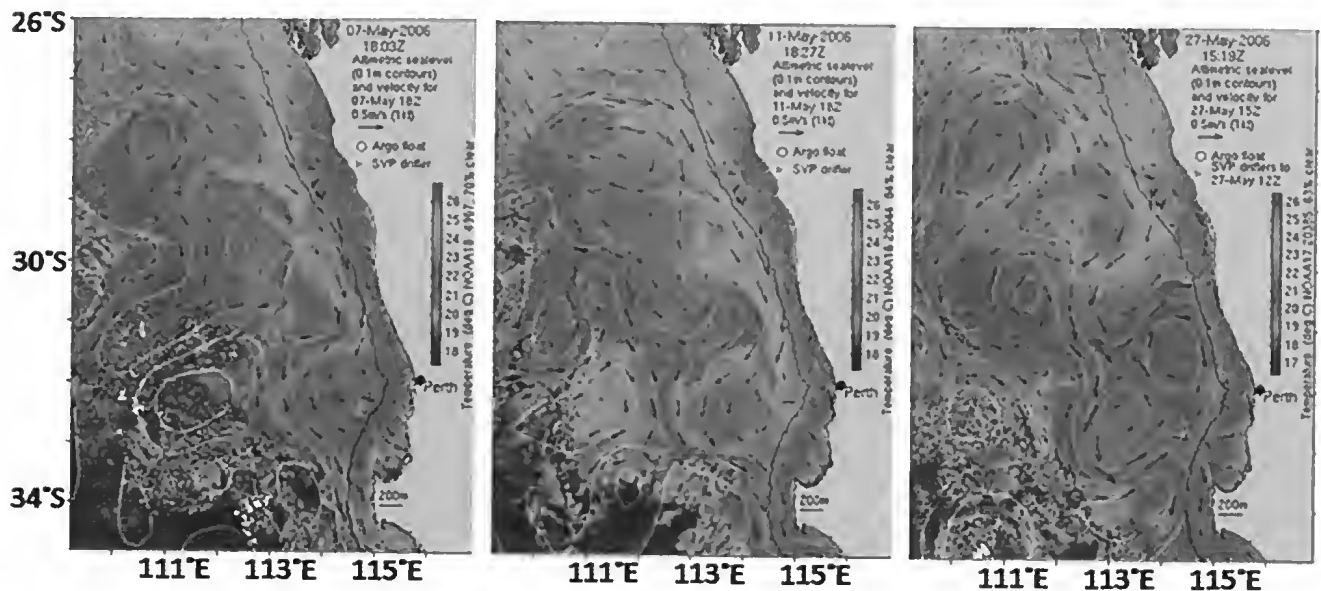


Figure 1. Satellite sea surface temperature images showing the development of an anticyclonic eddy at 32°S from 7–27 May 2006 within the south-east Indian Ocean (Source: www.oceancurrent.imos.org.au/).

Zooplankton samples were taken at 18 stations within the Leeuwin Current, the meander/ developing eddy, adjacent shelf and surrounding oceanic waters (Fig. 2). The locations of sampling stations were primarily determined by the trajectories of Iridium satellite-tracked drifting buoys (Fastwave Communications Pty Ltd), which were deployed during the voyage, as well as the use of near real time satellite imagery (sea surface temperature and surface chlorophyll *a*). The imagery aided in the distinction of eddy (centre and perimeter), adjacent continental shelf, Leeuwin Current and surrounding oceanic waters (Paterson *et al.* 2008; Holliday *et al.* 2011).

A conductivity-temperature-depth-oxygen (CTD-O2) instrument was used to measure vertical profiles of the water column immediately prior to zooplankton sampling. The Seabird SBE 19+ CTD-O2 was also equipped with a Chelsea TGI fluorometer to measure fluorescence, a proxy for chlorophyll *a*, and was cast from the surface to 500 m depth, or to ~ 10 m above the sea bottom for shelf stations. The mixed layer depth was determined when a change in potential density of 0.125 kg m^{-3} from that at 10 m depth occurred (Levitus 1982; Feng *et al.* 2007).

Zooplankton samples were collected at night using a 1 m^2 , multiple opening and closing EZ net equipped with a General Oceanics flowmeter (10 nets, mesh size of $335 \mu\text{m}$); this technique has been successfully used for collecting depth-stratified samples of fish larvae in this region (Muhling & Beckley 2007; Muhling *et al.* 2007). Two replicate tows were conducted to 200 m depth or to ~10 m above the seafloor on the shelf for all stations except P1, LC2, P5 and O13. Samples were preserved in a 5% buffered formalin seawater solution. For the purposes of this paper in documenting the euphausiid assemblages of the region, abundances of euphausiids at each station were derived by integrating the concentrations from each depth stratum, and were expressed as the number under 1 m^2 .

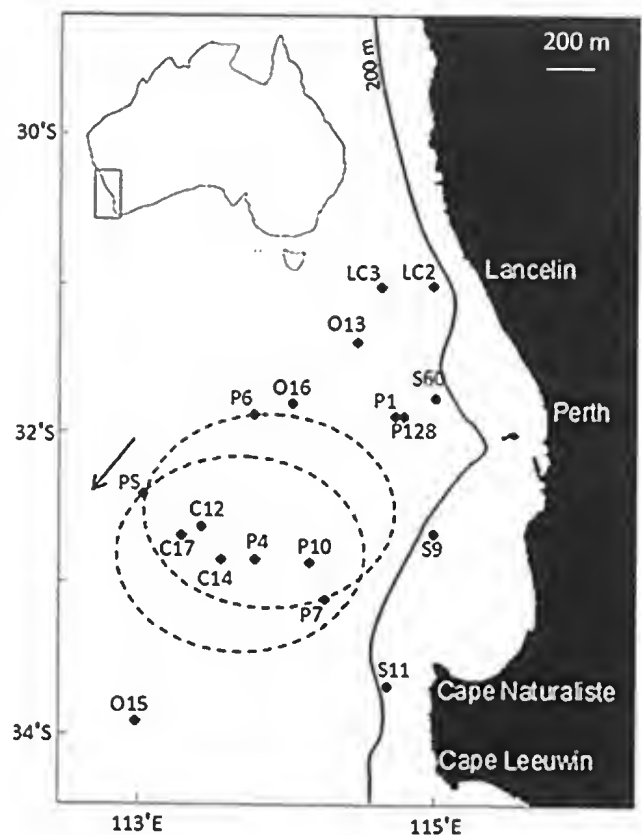


Figure 2. Location of stations within and around the Leeuwin Current anticyclonic eddy (dashed lines) where euphausiid samples were collected (adapted from Holliday *et al.*, 2011). Arrow indicates the propagation direction of the eddy. Letters correspond to station groupings for statistical purposes: LC = Leeuwin Current; P = eddy perimeter; C = eddy centre; S = shelf, O = oceanic.

With the aid of a Folsom plankton splitter to subsample (Gibbons 1999) and relevant taxonomic keys (Baker *et al.* 1990; Gibbons 1999), adult and juvenile euphausiids were counted and identified to species level. A minimum of 100 specimens were identified from the subsamples before an estimate of the whole sample was made. Damaged or indistinguishable juvenile specimens were grouped as unidentified. The difficult “*Euphausia gibba* species complex” comprises *Euphausia gibba* Sars 1883, *Euphausia paragibba* Hansen 1910, *Euphausia pseudogibba* Ortmann 1893, and *Euphausia hemigibba* Hansen 1910, and distinguishing between species is only based on minute morphological features (Baker *et al.* 1990) that could not be definitively recognised in all specimens. As *E. hemigibba* occurs throughout the south-east Indian Ocean (Brinton *et al.* 2000) and along the 110°E meridian (McWilliam 1977), specimens from this group were ascribed to this species in this study. The species pair *Thysanopoda astylata* and *Thysanopoda aequalis* is also difficult to distinguish and, in this study, thickness of the frontal plate was used, in addition to the defining feature of a flagellum-like spine on the third thoracic leg in adult males of *T. aequalis* (Baker *et al.* 1990).

Statistical analyses

For statistical analyses, stations were grouped *a priori* depending on their location within the eddy field, and were classified as Leeuwin Current meander/ eddy perimeter, eddy centre, oceanic, or shelf as per Holliday *et al.* (2011). As the study was of a Lagrangian design, it is recognised that the *a priori* locations were not represented by an equal number of stations, which could present a bias towards the observed species richness of Leeuwin Current meander/ eddy perimeter stations. Euphausiid assemblage structure (excluding unidentified and damaged specimens) across the eddy field was examined using the Primer-6 software package (Clarke & Gorley 2006) and, prior to analysis, data were fourth root transformed and a Bray-Curtis resemblance matrix was constructed. Non-metric multidimensional scaling ordination plots (nMDS) were used to assess the spatial relationships among euphausiid assemblages within, and among, sampling locations. A one-way analysis of similarity (ANOSIM) was then applied to determine significant spatial differences between euphausiid assemblages in relation to location, and a one-way similarity percentage routine (SIMPER) was used to show the dissimilarities of the assemblages between each of the locations.

A multivariate multiple regression analysis, using the distance-based linear modelling technique (DistLM) (Anderson 2001) was used to evaluate the relationship between water column properties (predictors) and euphausiid assemblages (response matrix). Mean values for the mixed layer of temperature, salinity, fluorescence, dissolved oxygen, surface chlorophyll *a* and depth were used by the model to determine how much variation in euphausiid assemblages was explained by the variation in water column properties. Prior to the analysis, data for the water column properties were examined using a draftsman scatter plot to determine appropriate data transformations according to the skewness and curvilinearity of the data (Clarke & Ainsworth 1993). Temperature was subjected to a log (*x*+1) transformation, all variables were normalised and a resemblance matrix

was constructed using Euclidean distance. Subsequently, salinity was removed from the analysis because of its strong negative correlation with temperature. Results were represented in a two-dimensional distance-based redundancy (dbRDA) biplot, in which the water column properties identified in the DistLM were used to constrain the ordination of euphausiid assemblages.

RESULTS

The studied anticyclonic eddy was formed from a meander of the Leeuwin Current during April 2006 and was sampled during its developing phase from 2–28 May (Paterson *et al.* 2008; Holliday *et al.* 2011) (Fig. 1). Most of the Leeuwin Current's volume was deflected offshore to circulate around the eddy perimeter and feed into the eddy. The eddy's connection with Leeuwin Current and shelf waters, as it developed from the meander, was evident from the strong cross shelf exchange observed in synoptic sea surface temperature and chlorophyll *a* data. Mixing between the eddy and surrounding water masses was responsible for the modification of the physiochemical and biological signature of the eddy (Paterson *et al.* 2008).

Holliday *et al.* (2011) identified three distinct water masses within the eddy field based on temperature and salinity properties, Leeuwin Current (> 23.0°C, < 35.4 psu), modified Leeuwin Current (21.5–22.5°C, 34.4–35.7 psu), and Sub-Tropical Surface Water (18–20.5°C, 35.8–35.9 psu) (Table 1). Leeuwin Current water was identified upstream of the eddy (LC2 & LC3), whilst the eddy centre and Leeuwin Current meander/ eddy perimeter stations were characterised by modified Leeuwin Current water, indicative of the mixing and water exchange with surrounding source waters. Oceanic stations (O13, O15 & O16) were characterised by Sub-Tropical Surface Water. Mixed layer depths varied across the eddy field, with shelf and eddy stations having a more homogenous water column structure. Eddy centre stations had deeper mixed layers, deepening with development from 70 m at E12 (16-May) to 119 m at E17 (22-May). Relatively high nutrient and chlorophyll *a* concentrations were also identified within the eddy (Paterson *et al.* 2008).

Twenty two euphausiid species from seven genera were identified from the 18 stations that were sampled within the eddy field (Table 1). Assemblages were dominated by *E. recurva*, *Stylocheiron carinatum* Sars 1883 and *P. latifrons*. *Euphausia sanzoi* Torelli 1934 and *T. astylata* Brinton 1975 have not previously been recorded for the south-east Indian Ocean, and are new records for the region. Furthermore, *Nematobrachion flexipes* (Ortmann 1893), *Stylocheiron microphthalmum* Hansen 1910, *Stylocheiron sulmi* Sars 1883, *T. aequalis* Hansen 1905 and *Nematoscelis microps* Sars 1883 have been reported for the south-east Indian Ocean, but are new records for Australian Exclusive Economic Zone. Within Australian waters, *P. latifrons*, *Nematoscelis atlantica* Hansen 1910, *Stylocheiron abbreviatum* Sars 1883, *Stylocheiron affine* Hansen 1910, *S. carinatum*, *Thysanopoda monacantha* Ortmann 1893 and *Thysanopoda tricuspidata* Milne-Edwards 1837 represent new distribution records for the southerly latitudes encompassed by the eddy (31–34°S). Previously, their distributions were regarded as restricted to lower latitudes (Davies 2002).

Table 1. Euphausiid species and mean abundance (number under $1\text{ m}^2 \pm \text{SE}$ down to 200 m, or 80 m for shelf stations S9 and S11) within the Leeuwin Current eddy field, and their documented geographic distributions as per Brinton et al. (2000). Total number of each species examined per replicate per location are also given (#). ¹ indicates a new record for the south-east Indian Ocean, ² indicates a new record for the Australian Exclusive Economic Zone, and ³ indicates new distribution records within the 31–34°S range of the Leeuwin Current eddy (Davie, 2002).

Species	LC/eddy perimeter 18			Eddy centre 6			Oceanic 6			Shelf 6			Geographic distribution
	Mean (m ²)	S.E.	#	Mean (m ²)	S.E.	#	Mean (m ²)	S.E.	#	Mean (m ²)	S.E.	#	
<i>Euphausia hemigibba</i>	12.2	3.5	494	10.9	3.1	181	7.7	0.6	165	0	—	0	Tropical/subtropical
<i>Euphausia nutica</i>	6.9	1.5	136	7.0	1.6	73	0.7	0.4	15	0.1	0.06	3	Tropical/subtropical
<i>Euphausia recurva</i>	135.5	22.3	5097	89.3	22.1	1322	31.4	8.8	670	1.2	0.7	28	Subtropical
<i>Euphausia sanzoi</i> ¹	0.1	0.1	10	0.3	0.1	8	0.2	0.1	5	7.2	6.1	107	Tropical/subtropical
<i>Euphausia similis</i>	6.1	2.2	145	1.0	0.3	12	2.6	1.0	72	0.2	0.2	6	Cosmopolitan
<i>Euphausia spinifera</i>	0.04	0.04	1	0	—	0	0.2	0.1	7	0	—	0	Subtropical
<i>Nematobrachion flexipes</i> ²	0.5	0.3	12	0	—	0	0.2	0.1	6	0	—	0	Tropical/subtropical
<i>Nematoscelis atlantica</i> ³	3.1	0.9	122	0.8	0.4	14	3.8	1.3	113	0	—	0	Subtropical
<i>Nematoscelis microps</i> ²	0.3	0.3	14	0	—	0	0.04	0.04	1	0	—	0	Tropical/subtropical
<i>Nematoscelis</i> spp.	6.9	1.5	298	3.0	0.9	61	5.8	1.6	176	0.3	0.3	3	Tropical/subtropical
<i>Pseudoeuphausia latifrons</i> ³	30.8	10.3	457	52.8	40.6	235	4.5	2.7	52	52.1	14.0	655	Tropical/subtropical
<i>Stylocheiron abbreviatum</i> ³	8.8	1.5	398	7.1	2.9	130	5.0	0.7	139	0.9	0.6	15	Tropical/subtropical
<i>Stylocheiron affine</i> ³	6.4	1.3	168	6.5	1.1	123	3.2	0.8	89	2.0	1.3	42	Tropical/subtropical
<i>Stylocheiron carinatum</i> ³	70.5	12.2	2195	63.7	11.8	924	15.8	3.5	289	25.3	10.1	403	Tropical/subtropical
<i>Stylocheiron microphthalma</i> ²	0.1	0.1	30	0.4	0.3	3	0	—	0	0.1	0.1	3	Tropical
<i>Stylocheiron subui</i> ²	20.4	2.5	774	23.5	4.3	375	5.0	0.4	99	10.1	4.4	136	Tropical/subtropical
<i>Stylocheiron</i> spp.	41.4	13.3	1294	17.7	6.4	254	5.9	1.9	119	7.7	2.8	142	Tropical/subtropical
<i>Thysanoessa gregaria</i>	1.0	0.5	178	0.4	0.2	7	2.7	1.2	91	0	—	0	Subtropical/temperate
<i>Thysanopoda aequalis</i> ²	0.3	0.2	17	0.4	0.2	21	0.3	0.1	8	0	—	0	Tropical/subtropical
<i>Thysanopoda astylata</i> ¹	0.6	0.2	38	1.3	0.4	69	0.4	0.2	62	0	—	0	Tropical
<i>Thysanopoda monacantha</i> ³	0.3	0.1	5	0	—	0	0.04	0.04	1	0	—	0	Tropical/subtropical
<i>Thysanopoda pectinata</i>	0	—	0	0.1	0.1	1	0	—	0	0	—	0	Tropical/subtropical
<i>Thysanopoda obtusifrons</i>	0.3	0.2	17	0.1	0.1	2	0.1	0.04	3	0	—	0	Tropical/subtropical
<i>Thysanopoda tricuspidata</i> ³	0	—	1	0.1	0.1	1	0.04	0.04	1	0.02	0.02	1	Tropical/subtropical
<i>Thysanopoda</i> spp.	4.1	0.9	155	0.8	0.2	13	0.5	0.3	9	0.1	0.04	2	Tropical/subtropical
Unidentified specimens	71.9	11.2		81.6	14.5		40.0	10.2		62.4	19.3		
Total abundance	428.9			368.8			136.3			169.8			

Euphausiid species richness was similar at oceanic (20 species), Leeuwin Current meander /eddy perimeter (20 species) and eddy centre (18 species) locations, but only 11 species were identified in shelf waters (Table 1). Ten species were shared across the four locations. Some species, namely *N. flexipes*, *N. microps*, *S. microphthalma* and most of the *Thysanopoda* spp., were considered rare based on their low abundances and presence at only a few stations throughout the eddy field (Table 1).

Euphausia recurva was most abundant at Leeuwin Current meander/ eddy perimeter stations with a mean of 135.5 (s.e. ± 22.3) individuals under 1 m^2 down to 200 m (Table 1). Mean abundances were considerably lower for the shelf stations ($1.2 \pm 0.7 \text{ m}^{-2}$). *Stylocheiron carinatum* showed a similar trend of highest mean abundance at Leeuwin Current meander/ eddy perimeter stations ($70.5 \pm 12.2 \text{ m}^{-2}$), which was greater than at both shelf and oceanic stations. The shelf and eddy centre contained the highest mean abundances of *P. latifrons*, at $52.1 \pm 14 \text{ m}^{-2}$ and $52.8 \pm 40.6 \text{ m}^{-2}$, respectively; abundance of this species was considerably lower for oceanic stations at 4.5 ± 2.7 individuals under 1 m^2 down to 200 m depth.

Considering abundance by water mass, modified Leeuwin Current water had the highest total mean abundance of euphausiids under 1 m^2 ($380.3 \pm 43.8 \text{ m}^{-2}$), followed by Leeuwin Current water ($276.9 \pm 72.0 \text{ m}^{-2}$) and sub-tropical surface water ($138.6 \pm 22.9 \text{ m}^{-2}$) (Fig. 3).

Ordination showed a clear spatial separation of the euphausiid assemblage of shelf stations from the all other stations (Fig. 4). High within-group variability of the shelf assemblage is demonstrated by the considerable spatial separation between each of the shelf samples. The close grouping of Leeuwin Current meander /eddy perimeter, eddy centre and oceanic stations is indicative of their similar euphausiid assemblages. Overall, there was a significant difference between euphausiid assemblages (ANOSIM: R statistic = 0.425 ; $p = 0.008$) that was driven by strong separation of the shelf assemblage from all other locations within the eddy field. The shelf was significantly different from Leeuwin Current meander/eddy perimeter stations (R statistic = 0.93 ; $p = 0.005$), but there were no significant differences between any other pairwise tests of assemblages from the four location groups (Table 2).

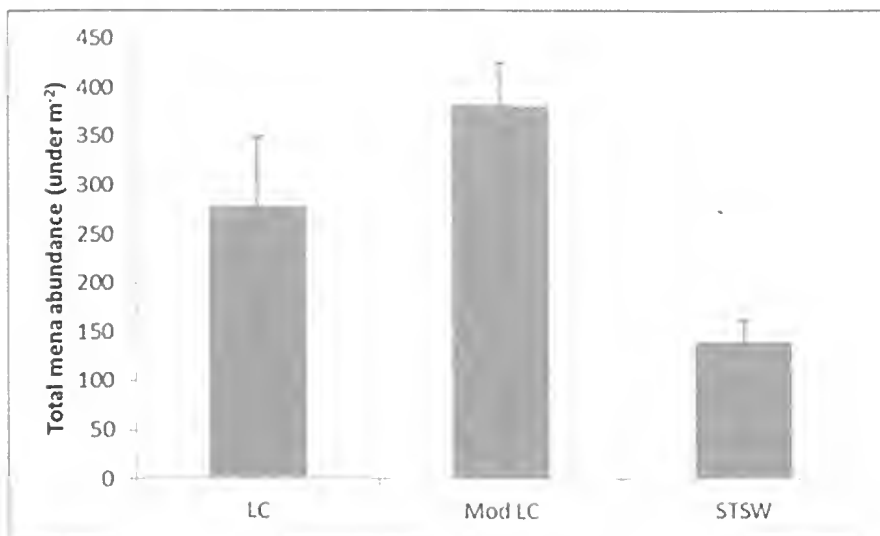


Figure 3. Total mean abundance of juvenile and adult euphausiids, under 1 m^2 , for Leeuwin Current water (LC), modified Leeuwin Current water (Mod LC) and Sub-Tropical Surface Water (STSW). Standard error bars are included.

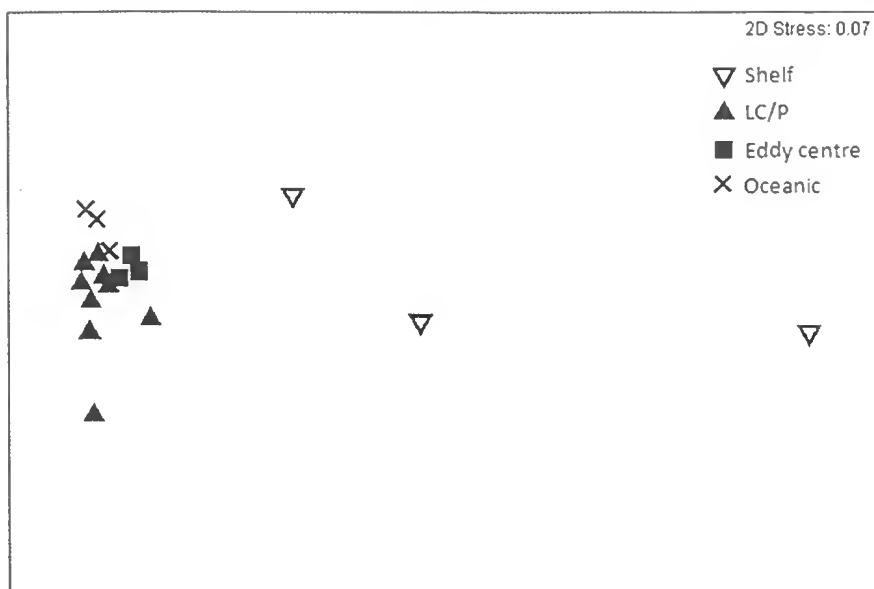


Figure 4. A two-dimensional nMDS ordination of euphausiid assemblages classified according to location in the Leeuwin Current eddy field, south-east Indian Ocean.

Table 2. One-way ANOSIM and SIMPER of euphausiid assemblages, according to *a priori* location groupings. Shading indicates the assemblage typical for each location; un-shaded are comparisons between locations, with significant differences marked with an asterisk. The four species contributing the highest abundances are listed for the location comparisons and superscript denotes the location in which each species was most common and abundant. Ave. Diss. = average dissimilarity, C = eddy centre, LC/P = Leeuwin Current meander/ eddy perimeter, O = oceanic, S = shelf.

	LC/ eddy perimeter	Eddy centre	Oceanic	Shelf
LC/eddy perimeter	Ave. Diss. = 21.9% <i>E. recurva</i> <i>Stylocheiron</i> spp. <i>S. carinatum</i> <i>S. suhmi</i>			
Eddy Centre	R= -0.06, p= 0.5 Ave. Diss. = 20.6%	Ave. Diss. = 14.4 % <i>E. recurva</i> <i>S. carinatum</i> <i>S. suhmi</i> <i>Stylocheiron</i> spp.		
Oceanic	R= 0.27, p= 0.12 Ave. Diss.= 24.1%	R= 0.93, p=0.10 Ave. Diss.= 20.4%	Ave. Diss. = 14.9% <i>E. recurva</i> <i>S. carinatum</i> <i>E. hemigibba</i> <i>S. suhmi</i>	
Shelf	*R= 0.93, p= 0.005 Ave. Diss.= 50.6% <i>E. recurva</i> ^(LC/P) <i>E. hemigibba</i> ^(LC/P) <i>Stylocheiron</i> spp. ^(LC/P) <i>Thysanopoda</i> spp. ^(LC/P)	R= 0.48, p= 0.10 Ave. Diss.= 47.4%	R= 0.59, p=0.10 Ave. Diss. = 51.3%	Ave. Diss. = 43.9% <i>P. latifrons</i> <i>S. carinatum</i> <i>S. suhmi</i>

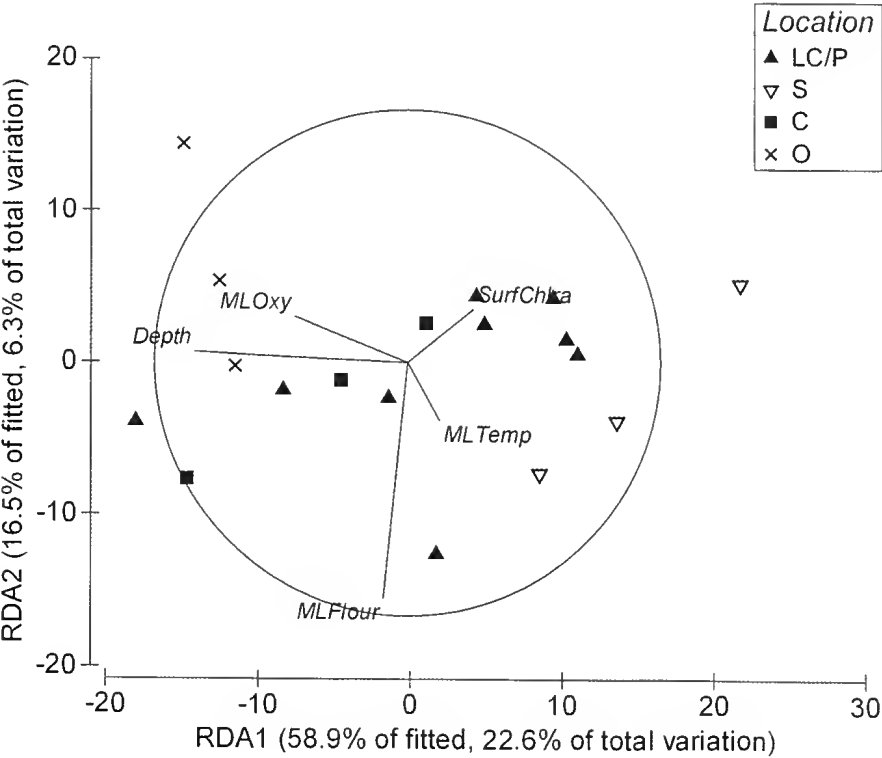


Figure 5. Explanation of the variation in euphausiid abundances across location using water column properties in a distance-based redundancy (dbRDA) biplot, including depth, mixed layer mean oxygen (MLOxy), mixed layer mean fluorescence (MLFlour), mixed layer mean temperature (MLTemp), and surface chlorophyll a (SurfChla).

Of the six water column properties used in the distance-based linear model, 29% of the total variance in euphausiid assemblages was accounted for, of which 19% was explained by depth ($p = 0.001$) (Fig. 5).

DISCUSSION

There have been few dedicated studies on euphausiids, or more broadly, zooplankton over the continental shelf and slope regions of the south-east Indian Ocean (Koslow *et al.* 2008). This study of the Leeuwin Current eddy field, encompassing shelf, slope and oceanic waters from 31°–34°S yielded 22 euphausiid species, including two new records for the south-east Indian Ocean and several new records for the Australian EEZ. Of the euphausiid species identified in this study, 17 have been previously identified along the 110°E meridian in oceanic waters about 200 km west of the study area (McWilliam 1977), and 12 previously identified off the north-west of Australia (Taniguchi 1974; Wilson *et al.* 2003). Of the numerically dominant species found in the eddy field, *E. recurva* is considered an oceanic species occurring in the subtropics of all ocean basins, and *S. carinatum* is typically epipelagic, occurring globally from 40°N to 40°S (Brinton 1975).

The third most numerically abundant euphausiid species, *P. latifrons*, is described as a neritic, tropical species with some records in the subtropics on the east and west coast of Australia (Brinton 1975; Brinton *et al.* 2000). Off the north-west shelf of Australia (21°–23°S), *P. latifrons* dominated euphausiid catches (> 98%) (Wilson *et al.* 2003) and the current study shows a high abundance of *P. latifrons* in shelf waters off temperate south-western Australia (30°–34°S). Although not yet examined, it is suspected that the distribution of this typically tropical shelf species could extend along the entire temperate shelf region, in line with the southward flow of the Leeuwin Current. Indeed, *P. latifrons* has been recorded at 29°–32°S in the neritic zone off South Africa (Gibbons 1997), which is under the influence of the southward flowing Agulhas Current system.

Two species, *E. sanzoi* and *T. astylata*, although occurring in low numbers, are new records for the south-east Indian Ocean. Described as having a tropical/ sub-tropical distribution, *E. sanzoi* occurs in the western Indian Ocean, eastern Indonesian Archipelago, the Philippines and north-east Australia (Brinton 1975). *Thysanopoda astylata*, a tropical species, is distributed throughout the Pacific Ocean but is typically restricted to north of the equator in the Indian Ocean. In both cases, flow of Pacific waters through the Indonesian Archipelago (Indonesian Throughflow) and subsequent inclusion into the catchment of the Leeuwin Current (Domingues *et al.* 2007) would facilitate southward dispersal of these species.

Although occurring at oceanic and eddy stations, species such as *T. aequalis* and *Thysanoessa gregaria* Sars 1883, were not recorded from shelf or Leeuwin Current stations to the north (LC2 and LC3). The distribution of these two species, previously reported in oceanic waters along the 110°E meridian (McWilliam 1977), suggests their entrainment from the surrounding oceanic sub-tropical surface waters adjacent to the eddy.

Entrainment of shelf waters into the developing eddy, could aid in the offshore transport of euphausiids, as found for larvae of neritic fish species (Holliday *et al.* 2011, 2012) and the picoplankton *Synechococcus* spp. (Paterson *et al.* 2013). *Pseudeuphausia latifrons*, typically a coastal species (Brinton 1975), was found in higher concentrations on the shelf and in the eddy centre, with oceanic and Leeuwin Current stations having the lowest concentrations. The high concentrations of *P. latifrons* within the eddy were probably derived from the direct entrainment of shelf waters containing previously accrued *P. latifrons*.

Given that there was no significant variability in euphausiid assemblages amongst eddy centre, Leeuwin Current meander/ eddy perimeter and oceanic stations, and that Paterson *et al.* (2008) showed the water masses at the four locations had similar water column properties, the lack of significant explanation from environmental variables was not unexpected. With the inclusion of depth as an explanatory variable, 19% of the variation amongst euphausiid assemblages was low, but significantly explained. In the same eddy field, shelf assemblages of meroplanktonic larval fishes were significantly different from those in the rest of the eddy field (Holliday *et al.* 2011) because of higher species richness, rather than lower species richness as found for holoplanktonic euphausiids.

Despite this being a short term study of a meso-scale feature of the Leeuwin Current system, 22 euphausiid species were identified. Bearing in mind survey effort, this equates to about half the number of species reported for other boundary current systems in the southern hemisphere. To date, forty species have been reported for the poleward flowing Agulhas Current in the south-west Indian Ocean within a similar latitudinal range to this study (Gibbons 1997; Gibbons *et al.* 1995). In total, 49 species have been recorded for the equatorward flowing Benguela Current system in the South Atlantic, of which 33 occurred within the same latitudinal range as this study. If indeed the number of euphausiid species is relatively low off temperate south-western Australia, this could be a reflection of the highly oligotrophic conditions when compared to other southern hemisphere boundary current systems (Pearce 1991). The pressure gradient driving the Leeuwin Current southwards (Cresswell & Golding 1980) is enough to suppress large scale and locally driven upwelling (Lourey *et al.* 2006; Twomey *et al.* 2007).

Euphausiid abundances throughout the Leeuwin Current eddy field during autumn did not indicate any evidence of swarming. These findings agree with S  wstr  m *et al.* (2014) who investigated the prey field for phyllosoma larvae and reported relatively low concentrations of euphausiids within the Leeuwin Current between 28°–32°S during July 2010. Euphausiids have been known to reach swarming concentrations of 10,000–500,000 individuals m⁻³ (O'Brien 1988; Murphy 2001; Guevara *et al.* 2008) and such swarms have been linked to reproduction (Mauchline & Fisher 1969; O'Brien 1988), temperature (Komaki 1967) and food (O'Brien 1988). However, aside from swarming events, euphausiids generally occur at much lower concentrations in the water column (Murphy 2001) although areas of upwelling can support substantially higher numbers of particular species.

For example, Pillar *et al.* (1989) recorded *Euphausia lucens* Hansen, 1905 in abundances of over 13,000 individuals under 1 m² down to 70 m in the Benguela upwelling system off South Africa. In the northern hemisphere, off Baja California within the California Current and using a bongo net tow from 210 m depth to the surface, Gomez-Gutierrez *et al.* (1995) found the dominant *Nyctiphanes simplex* Hansen 1911 at abundances of over 450 individuals under 1 m². Aside from *N. simplex*, all other species of euphausiids occurred at relatively low abundances, comparable to those observed for the Leeuwin Current eddy field. The Benguela and California Currents are both major upwelling areas and the studies indicated above were undertaken in autumn after the summer upwelling period.

As the Leeuwin Current is generally oligotrophic, primary production is low and typically dominated by smaller phytoplankton and microbes (Hanson *et al.* 2007). Interestingly, patches of chlorophyll *a* do occur in the south-east Indian Ocean, often within anticyclonic eddies where populations of coastal diatoms have been entrained (Thompson *et al.* 2007; Waite *et al.* 2007b; Moore *et al.* 2007). Likewise, these anticyclonic eddies have been observed to support greater abundances of meso-zooplankton such as chaetognaths, copepods and euphausiid larvae (Strzelecki *et al.* 2007). The developing anticyclonic eddy from this study contained higher chlorophyll *a* concentrations (Paterson *et al.* 2008) and higher abundances of the picoplankton *Synechococcus* spp. than the surrounding waters (Paterson *et al.* 2013). For the majority of euphausiid species in the eddy field, the eddy perimeter and eddy centre stations had greater abundances than the shelf and oceanic stations. As diatoms and microbes are known food sources for euphausiids (Quetin & Ross 1991; Cadée *et al.* 1992; Bargu & Silver 2003; Murphy *et al.* 2006), the higher abundances of euphausiids within the eddy may be linked to a greater abundance of such prey organisms.

Previous investigations of an eddy pair in the south-east Indian Ocean showed increased primary production and chlorophyll *a* in a Leeuwin Current warm core eddy compared to the cold core eddy (Thompson *et al.* 2007; Waite *et al.* 2007c). The increased productivity observed within Leeuwin Current warm core eddies is considered unusual given that cold core eddies are typically more productive as a result of the upwelling of nutrient rich waters (Falkowski *et al.* 1991; McGillicuddy & Robinson 1997; Bidigare *et al.* 2003). Similarly, the warm core Haida eddies formed in the North Pacific Ocean carry enhanced productivity and high levels of chlorophyll derived from coastal waters to surrounding offshore oceanic waters (Mackas & Galbraith 2002; Crawford *et al.* 2005). Warm core eddies are important meso-scale features and appear to provide a productive area in which entrained zooplankton, such as euphausiids, can accumulate and survive, particularly within an oligotrophic environment such as the south-east Indian Ocean.

CONCLUSIONS

Within the studied eddy field, 22 species of euphausiids were identified, which is more than double the number expected by Davie (2002). Several species have never before been recorded for Australian waters in the south-

east Indian Ocean. These included species that have previously only been recorded for the north-west shelf of Australia, and point to the Leeuwin Current as a potential vector for southward dispersal. In general, euphausiid abundances were relatively low and this was ascribed to the oligotrophic conditions off the coast of Western Australia. This was the first study to investigate euphausiid distributions within an evolving anticyclonic eddy in the south-east Indian Ocean and revealed the influence of mixing processes associated with the meso-scale feature on holoplanktonic euphausiids.

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REFERENCES

- ANDERSON M J 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26, 32–46.
- BAKER A DE C, BODEN P & BRINTON E 1990. *A practical guide to euphausiids of the world*. British Museum (Natural History), London.
- BARGU S & SILVER M W 2003. Field evidence of krill grazing on the toxic diatom genus *Pseudo-nitzschia* in Monterey Bay, California. *Bulletin of Marine Science* 72, 629–638.
- BRINTON E 1975. Euphausiids of southeast Asian waters, Naga Report. *Scientific results of marine investigations of the South China Sea and the Gulf of Thailand* 4 1–287.
- BRINTON E, OHMAN M D, TOWNSEND A W, KNIGHT M D & BRIDGEMAN A L 2000. *Euphausiids of the World Ocean World Biodiversity Database CD-ROM Series*. Springer UNESCO.
- BIDIGARE R R, BENITEZ-NEELSON C, LEONARD C L, QUAY P D, PARSONS M L, FOLEY D G & SEKI M P 2003. Influence of a cyclonic eddy on microheterotroph biomass and carbon export in the lee of Hawaii. *Geophysical Research Letters* 30, 1318–1322.
- CADÉE G C, GONZALEZ H & SCHINACK-SCHIEL S B 1992. Krill diet affects faecal string settling. *Polar Biology* 12, 75–80.
- CLARKE K R & AINSWORTH M 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* 92, 205–219.
- CLARKE K R & GORLEY R N 2006. *Primer v6: User Manual/ Tutorial*. PRIMER-E Ltd, Plymouth.
- CRAWFORD W R, BRICKLEY P J, PETERSON T D & THOMAS A C 2005. Impact of Haida Eddies on chlorophyll distribution in the Eastern Gulf of Alaska. *Deep-Sea Research II* 52, 975–989.
- CRESSWELL G R & GOLDING T J 1980. Observations of a south-flowing current in the southeastern Indian Ocean. *Deep-Sea Research* 27A, 449–466.
- DAVIE P 2002. Crustacea: Malacostraca: Phyllocarida, Hoplocarida, Eucarida (Part 1). In: Wells A & Houston W W K (eds) *Zoological Catalogue of Australia Vol. 19.3A*, pp. 96–111. CSIRO Publishing, Melbourne.
- DOMINGUES C M, MALTRUD M E, WIJFFELS S E, CHURCH J A & TOMCZAK M 2007. Simulated Lagrangian pathways between the Leeuwin Current System and the upper-ocean circulation of the southeast Indian Ocean. *Deep-Sea Research II* 54, 797–817.

- FALKOWSKI P G, ZIEMANN D, KLBER Z, & BIENFANG P K 1991. Role of eddy pumping in enhancing primary production in the ocean. *Nature* **353**, 55–58.
- FANG F & MORROW R 2003. Evolution, movement and decay of warm-core Leeuwin Current eddies. *Deep-Sea Research II* **50**, 2245–2261.
- FENG M, MAJEWSKI L, FANDRY C B & WAITE A M 2007. Characteristics of two counter-rotating eddies in the Leeuwin Current system off the Western Australian coast. *Deep-Sea Research II* **54**, 961–980.
- FENG M, MEYERS G, PEARCE A & WIJFFELS S 2003. Annual and interannual variations of the Leeuwin Current at 32°S. *Journal of Geophysical Research* **108**, 3355 doi:10.1029/2002JC001763.
- FENG M, SLAWINSKI D, BECKLEY L E & KEESING J K 2010. Retention and dispersal of shelf waters influenced by interactions of ocean boundary current and coastal geography. *Marine and Freshwater Research* **61**, 1259–1267.
- FOX N J & BECKLEY L E 2005. Priority areas for conservation of Western Australian coastal fishes: A comparison of hotspot, biogeographical and complementarity approaches. *Biological Conservation* **125**, 399–410.
- GIBBONS M 1997. Pelagic biogeography of the South Atlantic Ocean. *Marine Biology* **129**, 757–768.
- GIBBONS M 1999. *An introduction to the zooplankton of the Benguela Current region*. Ministry of Fisheries and Marine Resources, Republic of Namibia.
- GIBBONS M, BARANGE M & HUTCHINGS L 1995. Zoogeography and diversity of euphausiids around southern Africa. *Marine Biology* **123**, 257–268.
- GOMEZ-GUTIERREZ J, PALAMARES-GARCIA R & GENDRON D 1995. Community structure of the euphausiid populations along the west coast of Baja California, Mexico, during the weak ENSO 1986–1987. *Marine Ecology Progress Series* **120**, 41–51.
- GUEVARA P L, LAVANIEGOS B E & HECKEL G 2008. Fin whales (*Balaenoptera physalus*) foraging on daytime surface swarms of the euphausiid *Nyctiphanes simplex* in Ballenas Channel, Gulf of California, Mexico. *Journal of Mammalogy* **89**, 559–566.
- HANSON C E, WAITE A M, THOMPSON P A & PATTIRATCHI C B 2007. Phytoplankton community structure and nitrogen nutrition in Leeuwin Current and coastal waters off the Gascoyne region of Western Australia. *Deep-Sea Research II* **54**, 902–924.
- HOLLIDAY D, BECKLEY L, MILLAR N, OLIVAR M, SLAWINSKI P D, FENG M & THOMPSON P A 2012. Larval fish assemblage and particle back-tracking define latitudinal and cross-shelf variability in an eastern Indian Ocean boundary current. *Marine Ecology Progress Series* **460**, 127–144.
- HOLLIDAY D, BECKLEY L & OLIVAR M P 2011. Incorporation of larval fishes into a developing anti-cyclonic eddy of the Leeuwin Current off south-western Australia. *Journal of Plankton Research* **33**, 1696–1708.
- HUTCHINS J B & PEARCE A F 1994. Influence of the Leeuwin Current on recruitment of tropical reef fishes at Rottnest Island, Western Australia. *Bulletin of Marine Science* **54**, 245–255.
- KOMAKI Y 1967. On the surface swarming of euphausiid crustaceans. *Pacific Science* **21**, 433–448.
- KOSLOW J A, PESANT S, FENG M, PEARCE A, FEARNES P, MOORE T, MATEAR R & WAITE A 2008. The effect of the Leeuwin Current on phytoplankton biomass and production off Southwestern Australia. *Journal of Geophysical Research* **113**, C07050, doi:10.1029/2007JC004102.
- LEVITUS S 1982. *Climatological atlas of the world ocean*. NOAA Professional. Paper, 13, U.S. Govt. Printing Office, Washington, D.C.
- LOUREY M J, DUNN J R & WARING J 2006. Mixed-layer nutrient climatology of Leeuwin Current and Australian shelf waters: seasonal nutrient dynamics and biomass. *Journal of Marine Systems* **59**, 25–51.
- MACKAS D L & GALBRAITH M D 2002. Zooplankton distribution and dynamics in a North Pacific eddy of coastal origin: 1. Transport and loss of continental margin species. *Journal of Oceanography* **58**, 728–738.
- MAUCHLINE J & FISHER L R 1969. The biology of euphausiids. *Advances in Marine Biology* **7**, 1–454.
- MAXWELL J G H & CRESSWELL G R 1981. Dispersal of tropical fauna to the Great Australian Bight by the Leeuwin Current. *Australian Journal of Marine and Freshwater Research* **32**, 493–500.
- MCGILLICUDDY JR D J & ROBINSON A R 1997. Eddy-induced nutrient supply and new production in the Sargasso Sea. *Deep-Sea Research II* **44**, 1427–1450.
- MCWILLIAM P S 1977. Further studies of plankton ecosystems in the Eastern Indian Ocean VI. Ecology of the Euphausiacea. *Australian Journal of Marine and Freshwater Research* **28**, 627–644.
- MOORE II T S, MATEAR R J, MARRA J & CLEMENTSON L 2007. Phytoplankton variability off the Western Australian coast: mesoscale eddies and their role in cross-shelf exchange. *Deep-Sea Research II* **54**, 943–960.
- MUHLING B A & BECKLEY L E 2007. Seasonal variation in horizontal and vertical structure of larval fish assemblages off south-western Australia, with implications for larval transport. *Journal of Plankton Research* **29**, 967–983.
- MUHLING B A, BECKLEY L E & OLIVAR M P 2007. Ichthyoplankton assemblage structure in two meso-scale Leeuwin Current eddies, eastern Indian Ocean. *Deep-Sea Research II* **54**, 1113–1128.
- MURPHY E J 2001. Krill. *Encyclopaedia of Ocean Science* **3**, 1405–1413.
- MURPHY E J, WATKINS J L, TRATHAN P N, REID K, MEREDITH M P, THORPE S E, JOHNSTON N M, CLARKE A, TARLING G A, COLLINS M A, FORCADA J, SHREEVE S R, ATKINSON A, KORB R, WHITEHOUSE M J, WARD P, RODHOUSE P G, ENDERLEIN P, HIRST A G, MARTIN A R, HILL S L, STANILAND I J, POND D W, BRIGGS D R, CUNNINGHAM N J & FLEMING A H 2006. Spatial and temporal operation of the Scotia Sea ecosystems: a review of large-scale links in a krill centred food web. *Philosophical Transactions of the Royal Society B* **362**, 113–148.
- O'BRIEN D P 1988. Surface schooling behaviour of the coastal euphausiid *Nyctiphanes australis* (Crustacea: Euphausiacea) off Tasmania, Australia. *Marine Ecology Progress Series* **42**, 219–233.
- PATERSON H L, FENG M, WAITE A M, GOMIS D, BECKLEY L E, HOLLIDAY D & THOMPSON P A 2008. Physical and chemical signatures of a developing anticyclonic eddy in the Leeuwin Current, eastern Indian Ocean. *Journal of Geophysical Research* **113**, 1–14.
- PATERSON H L, HEEL K & WAITE A 2013. A warm-core eddy linking shelf, Leeuwin Current and oceanic waters demonstrated by near-shelf distribution patterns of *Synechococcus* spp. and *Prochlorococcus* spp. in the eastern Indian Ocean. *Marine and Freshwater Research* **64**, 1011–1021.
- PEARCE A F 1991. Eastern boundary currents of the southern hemisphere. *Journal of the Royal Society of Western Australia* **74**, 35–45.
- PEARCE A F, SLAWINSKI D, FENG M, HUTCHINS B & FEARNES P 2011. Modelling the potential transport of tropical fish larvae in the Leeuwin Current. *Continental Shelf Research* **31**, 2018–2040.
- PILLAR S C, ARMSTRONG D A & HUTCHINGS L 1989. Vertical migration, dispersal and transport of *Euphausia lucens* in the southern Benguela Current. *Marine Ecology Progress Series* **53**, 179–190.
- QUETIN L B & ROSS R M 1991. Behavioral and physiological characteristics of the Antarctic krill, *Euphausia superba*. *American Zoologist* **31**, 49–63.
- RIDGWAY K R & CONDIE S A 2004. The 5500-km-long boundary flow off western and southern Australia. *Journal of Geophysical Research* **109**, 1–18.

- RIVKIN R B 1991. Seasonal patterns of planktonic production in McMurdo Sound, Antarctica. *American Zoologist* **31**, 5–16.
- SÄWSTRÖM C, BECKLEY L E, SAUNDERS M I, THOMPSON P A, WAITE A M 2014. The zooplankton prey field for rock lobster phyllosoma larvae in relation to oceanographic features of the south-eastern Indian Ocean. *Journal of Plankton Research* **0**, 1–14.
- STRZELECKI J, KOSLOW J A & WAITE A 2007. Comparison of mesozooplankton communities from a pair of warm- and cold-core eddies off the coast of Western Australia. *Deep-Sea Research II* **54**, 1103–1112.
- TANIGUCHI A 1974. Mysids and euphausiids in the eastern Indian Ocean with particular reference to invasion of species from the Banda Sea. *Journal of Marine Biological Association of India* **16**, 349–357.
- THOMPSON P A, PESANT S & WAITE A M 2007. Contrasting the vertical differences in the phytoplankton biology of a dipole pair of eddies in the south-eastern Indian Ocean. *Deep-Sea Research II* **54**, 1003–1028.
- TWOMEY L J, WAITE A M, PEZ V & PATTIARATCHI C 2007. Variability in nitrogen uptake and fixation in the oligotrophic waters off the south west coast of Australia. *Deep-Sea Research II* **54**, 943–960.
- WAITE A M, PESANT S, GRIFFIN D A, THOMPSON P A & HOLL C M 2007c. Oceanography, primary production and dissolved inorganic nitrogen uptake in two Leeuwin Current eddies. *Deep-Sea Research II* **54**, 981–1002.
- WAITE A M, MUHLING B A, HOLL C M, BECKLEY L E, MONTOYA J P, STRZELECKI J, THOMPSON P A & PESANT S 2007b. Food web structure in two counter-rotating eddies based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic analyses. *Deep-Sea Research II*, **54**, 1055–1075.
- WAITE A M, THOMPSON P A, PESANT S, FENG M, BECKLEY L E, DOMINGUES C M, GAUGHAN D, HANSON C E, HOLL C M, KOSLOW T, MELLEENERS M, MONTOYA J P, MOORE T, MUHLING B A, PATERSON H, RENNIE S, STRZELECKI J & TWOMEY L 2007a. The Leeuwin Current and its eddies: an introductory overview. *Deep-Sea Research II* **54**, 789–796.
- WELLER E, HOLLIDAY D, FENG M, BECKLEY L & THOMPSON P 2011. A continental shelf scale examination of the Leeuwin Current off Western Australia during the austral autumn-winter. *Continental Shelf Research* **31**, 1858–1868.
- WILSON S G, MEEKAN M G, CARLETON J H, STEWART T C & KNOTT B 2003. Distribution, abundance and reproductive biology of *Pseudeuphausia latifrons* and other euphausiids on the southern North West Shelf, Western Australia. *Marine Biology* **142**, 369–379.

Diurnal Patterns in Phytoplankton Photosynthesis, Fremantle Harbour

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Phytoplankton are likely to be one of the main sources of autochthonous production in the Swan Canning estuary yet only limited published data are available on their photosynthetic dynamics. Here we describe the phytoplankton community composition at the mouth of the estuary and diurnal pattern of phytoplankton photosynthesis by applying chlorophyll fluorescence techniques. Diatoms were the dominant taxa (46–88% of the phytoplankton community) recorded throughout the sampling period although their dominance appeared to increase with the flood tide. A diurnal pattern in photosynthetic performance was apparent via chl-*a* fluorescence measurements. Night-time deactivation of Calvin-Benson cycle enzymes was evidenced by low $rETR_{max}$ and light saturation point (E_k ; minimum value of 207.5 ± 2.3 (se) $\mu\text{mol photon m}^{-2} \text{s}^{-1}$) values. Observed daytime increases in E_k (maximum value of 835.8 ± 3.8 (se) $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ at 4pm) with simultaneous reduction of α suggests dynamic down-regulation of PSII electron transport during the day. Maximum quantum yield of PSII (F_v/F_m) decreased from a value of 0.81 to minima of 0.51 during high-light periods of the day. Accounting for these dynamics is important in the design of future studies of phytoplankton productivity in the system. High recorded values of F_v/F_m and an unimpeded ability to photoregulate suggest the diatom-dominated marine phytoplankton community found in Perth's coastal waters at the time of this study was nutrient replete.

KEYWORDS: chlorophyll fluorescence, diurnal pattern, estuary, photoregulation, primary production, quantum yield

Abbreviations: α = initial slope of the photosynthesis vs irradiance curve; E_k = saturation irradiance; ETR = Electron Transport Rate; F' = chl-fluorescence level under actinic light; F_m = saturation pulse-induced maximum chl-fluorescence level from a dark-adapted sample when all photosystem II reaction centres are closed and non-photochemical quenching is negligible; F'_m = maximum chl-fluorescence level from a light-adapted sample exposed to a saturation pulse, closing all all photosystem II reaction centres; F_0 = minimum chl-fluorescence level from a dark-adapted sample when all photosystem II reaction centres are open; F_v = maximum variable fluorescence ($F_m - F_0$); F'_v = variable fluorescence under actinic light ($F'_m - F'$); F'_v/F'_m = maximum quantum yield of photochemistry at photosystem II; F'_v/F_m = effective quantum yield of photochemistry at photosystem II in the light; RCII = photosystem II reaction centre; $rETR$ = relative electron transport rate; $rETR_{max}$ = maximum relative electron transport rate.

INTRODUCTION

The city of Perth, Western Australia, surrounds the Swan-Canning Estuary. This microtidal, wave-dominated estuary is the second largest estuary in south-western Australia (Thompson 1998) and Fremantle Harbour is located at its mouth. Freshwater flow from tributaries is highly seasonal and a salt-wedge extends up the estuary from October to July/August (<http://www.wrc.wa.gov.au/srt/riverscience/>). The harbour is the transitional point between the oligotrophic coastal waters and the mesotrophic waters of the lower estuary.

Phytoplankton, microphytobenthos and seagrass are important sources of autochthonous production within the Swan-Canning Estuary (Hillman *et al.* 1995; Masini & McComb 2001) however there is a paucity of data on the photosynthetic dynamics of phytoplankton in the estuary and Perth coastal waters. While there have been some measurements of phytoplankton primary production (Thompson 1998), much of the literature has focused on the relationship between phytoplankton (chl-*a*, species composition) and environmental factors such as salinity, river flow, temperature and dissolved nutrients (Thompson 1998; Thompson 2001; Twomey & John 2001). Active chlorophyll fluorometry allows rapid estimation of photosynthetic parameters (e.g. quantum yield, electron transport rate) however the number of studies applying this technology to investigate diurnal patterns in phytoplankton photosynthesis *in situ* and with high sampling frequency is limited (Dijkman & Kromkamp 2006; Kurzbaum *et al.* 2010; Mackey *et al.* 2008; Verspecht 2007; Zhang *et al.* 2008).

Previous studies suggest that daily endogenous rhythms in the maximum rate of photosynthesis (P_{max}) and α occur in all major taxonomic groups of phytoplankton and that these rhythms are independent of changes in chl-*a* content (Harding *et al.* 1982; Boyd *et al.* 1997; Behrenfeld *et al.* 2004). Such rhythms should be taken into account when designing experiments investigating phytoplankton photosynthesis and interpreting results.

This study aims to describe the phytoplankton community present in Perth's coastal waters and investigate any diurnal pattern of photosynthesis by applying chlorophyll fluorescence techniques.

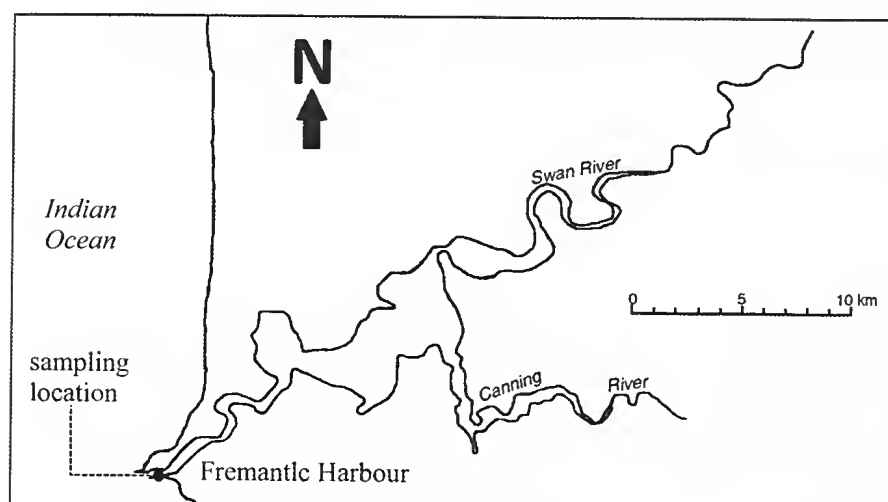


Figure 1. The study site on the seaward edge of Fremantle Harbour, the mouth of the Swan-Canning Estuary (modified from Hamilton *et al.* (2006)).

METHODS

Study site and environment

The study site was located at the mouth of Fremantle Harbour, with sample collection from a small motorised boat between the Maritime Museum of Western Australia and the OceanFarm jetty (Figure 1; GPS coordinates: 32°03'18.90" S 115°44'14.93" E). All sample collection and on-site measurements were performed on 7th December, 2005. Data on solar irradiance (W m^{-2}) incident at sea level were taken from Murdoch University meteorological station data (located 9.4 km from Fremantle Harbour; <http://www.met.murdoch.edu.au/downloads.htm>). These data were converted to photosynthetically available radiation (400–700 nm) in units of $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ following the method of Thompson (1998). Tidal information was collected from the Coastal Data Centre (<http://www.dpi.wa.gov.au/marine/coastaldata/1895.asp>) and on-site observations, while water surface temperature was recorded during each sampling occasion with a mercury thermometer.

Phytoplankton composition and chlorophyll

Samples for phytoplankton and chlorophyll were collected at 03:00 and every second hour until 19:00. A final sample was collected at 22:00 to yield a total of 10 samples for each analysis.

For phytoplankton identification and enumeration, at each sampling period a 1 L of near-surface (~0.5 m) seawater was collected from the end of the OceanFarm jetty into a thrice-rinsed Nalgene® bottle and 1 mL of Lugols iodine solution added. Analysis was performed using a Sedgewick-Rafter chamber at 200× magnification under a light microscope. Samples had previously been allowed to settle (>7 days) and concentrated 10–15 fold. Cell density calculation took concentration and dilution (due to addition of Lugols) into account. The most dominant phytoplankton were identified to species level using Tomas (1997), however in most instances cells were categorised into major taxonomic groupings only.

A further ~5 L near-surface (~0.5 m) grab sample was collected for chlorophyll-*a* determination. Samples were kept cool and in dim light until they could be returned to the university laboratory (no longer than 2 h) for

filtration through Whatman GF/F (45 mm) at a pressure of 40 ± 10 kPa. Filters were patted dry, wrapped in aluminium foil and frozen at -80°C for later extraction. Extraction was performed with ice-cold 90% (v/v) acetone by manual grinding using a glass mortar and pestle (modified from Strickland and Parsons (1972)). The homogenate was set in ice and away from light for 30 min and then clarified by centrifugation at 2100 rpm (1000 g) for 15 min in a Beckman GPR model centrifuge at 4°C . The centrifuge vials were then returned to ice and the supernatant used to determine chl-*a* content spectrophotometrically using the equations of Jeffrey and Humphrey (1975) for chromophyte algae containing chlorophylls *a*, *c*₁ and *c*₂. A Beckman DU-50 (UV-VIS) series spectrophotometer was used for all spectrophotometric measurements.

Chlorophyll fluorescence

Samples for chl-fluorescence measurements were collected from a small motorised boat using a 25 μm mesh-size phytoplankton net towed just below the surface until concentration of phytoplankton was sufficient to yield a satisfactory signal to noise ratio in the fluorometer. This generally took about 20–25 minutes. Upon return to the shore the suspension in the phytoplankton net cod-end was passed through a 180 μm mesh to remove zooplankton prior to sample measurements.

All fluorescence measurements were performed with a Water-PAM fluorometer (Walz, Germany) consisting of a Water-ED emitter-detector unit and a PAM-Control box. Data collection was via the WinControl (v2.08) software provided with the fluorometer. The fluorescence terminology used here follows that of Baker and Oxborough (2004). Samples were collected for fluorescence analysis on an hourly basis from 03:00 until 22:00 and were kept in dim light (shade) until measured.

Rapid light curves (RLCs) were performed to measure relative electron transport rate (rETR). Light levels were chosen, based on preliminary measurements (data not shown), to achieve a balance between maintaining as many points in the light-limited region of the curve while allowing an asymptote or down-turn to be evident. Gain levels were adjusted to maintain a dark fluorescence signal (i.e. measuring light only) of 200–300 units. Light

width at each irradiance was 5 s and saturation pulse duration was 0.8 s. For each sampling period ten replicate RLCs were performed on light adapted samples (kept in shaded conditions during collection procedure and during any delay before measurement). Ten replicate dark adapted F_v/F_m measurements were also collected at each sampling period. Dark-adaptation was for 15 minutes and samples were exposed to 5 s of far-red light immediately prior to applying the saturation pulse. rETR was calculated as (Cosgrove & Borowitzka 2010). Data were imported into Matlab® (Mathworks) and the model of Eilers and Peeters (1988) was fitted to the combined data (10 replicates) for each treatment to generate photosynthesis-irradiance (P-E) curve parameters. The error of the parameter estimates was derived from the covariance matrix of the fitted model and expressed as standard error.

RESULTS

Site conditions

Water temperature was 18°C during the early morning and late evening and 20°C throughout the day from 10:00 to 18:00. Lower temperatures coincided with ebb tide while higher temperatures occurred during flood tide.

Species composition, cell density and biomass (chl-a)

Diatoms (Bacillariophyceae) were found to be the

dominant taxon throughout the sampling period. Diatoms were most dominant in the evening, representing a maximum of 88% of the phytoplankton community at 22:00 and a minimum of 46% at 15:00 (Figure 2). The highest percentage of diatoms occurred close to the end of the flood tide. The large species *Chaetoceros lorenzianus* and *C. curvisetus* were dominant at 15:00 while the small species (unidentified and referred to as *Chaetoceros* sp1.) was dominant in the evening (Table 1). The most commonly abundant species during the sample period were: *Chaetoceros* sp1., *Pseudonitzschia seriata*, unidentified nanoflagellates and *C. curvisetus*. Due to the predominance of diatoms throughout the entire sampling period it was assumed that changes in species composition had negligible impact on chl-fluorescence measurements.

The chl-*a* concentration of the marine waters at the mouth of Fremantle Harbour increased throughout the day, reaching a peak of 2.54 µg L⁻¹ at 15:00 before decreased in the evening towards the end of flood tide. Average chl-*a* concentration across the entire sampling period was 1.73±0.18(se) µg L⁻¹ (n=9). While phytoplankton cell density was generally positively related with chl-*a* concentration, there were some periods where dominance of large (i.e. 13:00) or small (i.e. 22:00) species yielded relatively high or low chl-*a* concentrations, respectively (r^2 shifts from 0.066 (n=9) to 0.592 with these two sampling times removed; data not shown).

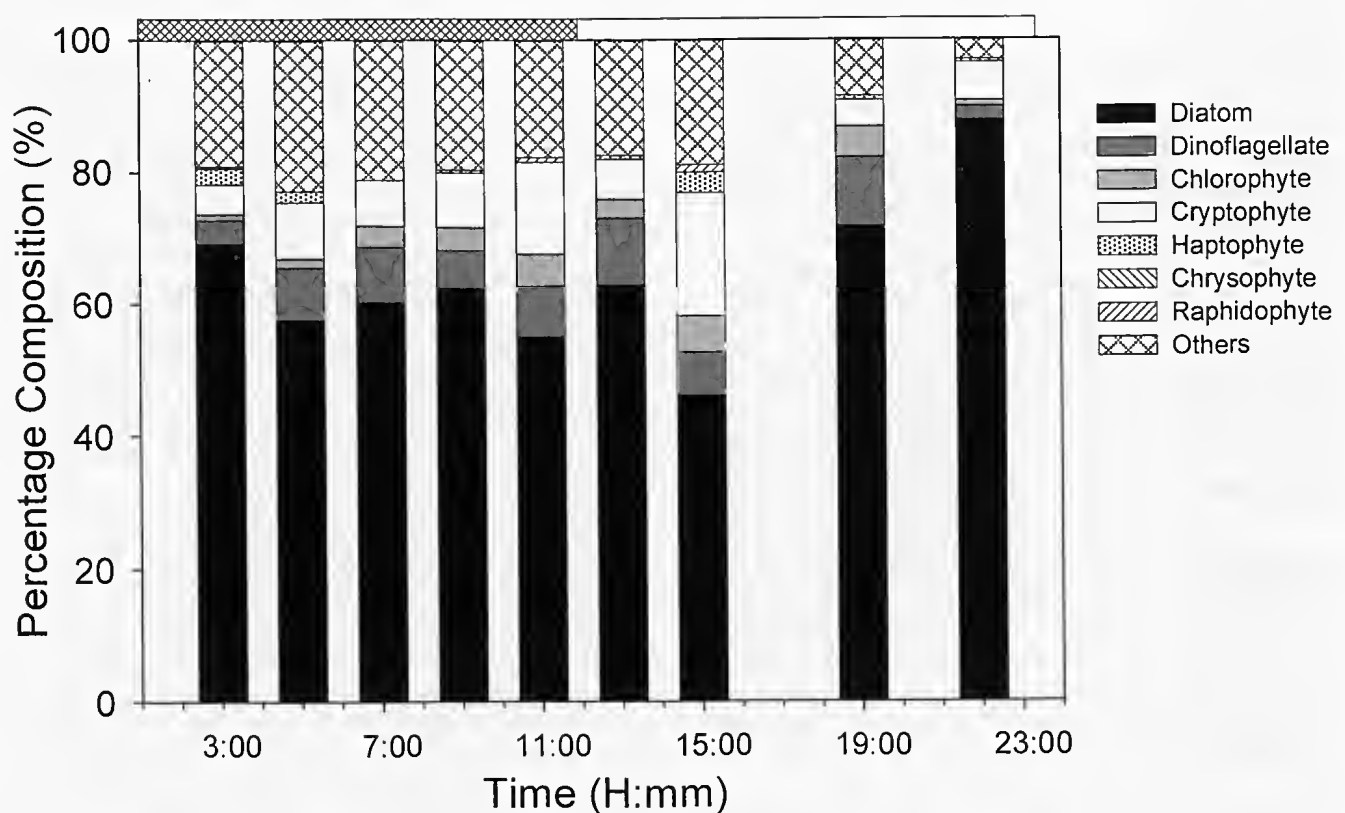


Figure 2. Percentage composition of phytoplankton taxa in Fremantle Harbour over the duration of the study period. Ebb tide is indicated by the thatched bar at the top of the graph while flood tide is indicated with an open bar.

Table 1. Fremantle Harbour phytoplankton community composition and relative abundance at ~0.5 m depth. Grab samples were collected every second hour throughout the day. (+) present, (++) present in moderate relative abundance, (+++) present at a high abundance relative to other species.

	3 AM	5 AM	7 AM	9 AM	11 AM	1 PM	3 PM	5 PM	7 PM	10 PM
Diatoms										
<i>Bacillaria cf. paradoxa</i>			+							
<i>Cerataulina</i> sp.	+						+		+	+
<i>Chaetoceros curvisetus</i>	+	+		+++	+++	+++	+++		+	+
<i>Chaetoceros cf. lorenzianus</i> var. <i>forceps</i>		+					+			
<i>Chaetoceros cf. laciniosus</i>			+		++	++	+++		++	
<i>Chaetoceros decipiens</i>				+	++	+			+	+
<i>Chaetoceros tenuissimus</i>						+				
<i>Chaetoceros</i> sp1.	+++	+++	+++	+++	++	+++	+++		+++	+++
<i>Cylindrotheca closterium</i>	+	+	+	+	+	+	+		++	+
<i>Cyclotella meneghiniana</i>				+	+	+	+			+
<i>Diploneis</i> sp.			+	+						
<i>Entomoneis</i> sp.	+	+	+	+		+				
<i>Guinardia</i> sp.										
cf. <i>Gyrosigma</i> sp.						+	+			
<i>Licmophora</i> sp.					+				+	
<i>Navicula</i> spp.	+	+	+	+	+	+	+		+	+
<i>Nitzschia</i> spp.	+	+					+		+	
<i>Pseudonitzschia seriata</i>	+++	+++	+++	+++	++	++	++		++	+++
<i>Pseudonitzschia pseudodelicatissima</i>	+	+							+	+
cf. <i>Roicosigma</i> sp.						+				
<i>Skeletonema costatum</i>	++	+	+++	+		+++			+	+
cf. <i>Striatella</i> sp.									+	
<i>Thalassionema</i> sp.	+	+	+	+	++	++	+		+	+
<i>Thalassiosira</i> spp.			+						+	
Dinoflagellates										
<i>Amphidinium</i> sp.			+			+	+		+	
<i>Ceratium furca</i>	+		+			+	+		+	+
<i>Dinophysis acuminata</i>					+					
<i>Diplopsalis</i> sp.						+				
<i>Gonyaulax</i> sp.										
<i>Gymnodinium</i> spp.		+	+	+	+	+	+		+	+
<i>Gyrodinium</i> spp.	+	+	+	+	+	+	+			
<i>Katodinium glaucum</i>	+				+					
<i>Katodinium rotundata</i>		+	+		+	+	+		+	+
<i>Polykrikos</i> sp.									+	
<i>Prorocentrum minimum</i>		+	+		+	+	+		+	+
<i>Prorocentrum micans</i>			+	+	+	+	+		+	+
<i>Prorocentrum triestinum</i>									+	+
<i>Protoperidinium</i> spp.	+		+		+	+			+	+
<i>Scrippsiella cf. trochoidea</i>	+	+					+		+	
Cryptophytes										
cf. <i>Plagioselmis</i> spp.		+	+	+	+	+	+		+	+
cf. <i>Rhodomonas</i> sp.					+					
cf. <i>Teleaulax</i> sp.	+		+			+	++		+	
Prasinophytes										
<i>Pyramimonas</i> spp.	+	+		+	+	+	+		+	+
<i>Tetraselmis</i> sp.		+	+	+	+		+		+	
Euglenoids										
<i>Eutreptiella</i> sp.		+	+		+					
Chrysophytes										
<i>Apedinella</i> sp.	+	+								
<i>Pseudopedinella</i> sp.	+	+		+		+	+		+	+
Raphidophytes										
<i>Heterosigma akashiwo</i>	+				+		+			
Silicoflagellates										
<i>Dictyocha fibula</i>		+	+							+
Others										
<i>Ebria tripartita</i>							+			
<i>Mesodinium rubrum</i>	+	+	+			+	+		+	+
Nanoflagellates	++	++	++	+++	++	++	+++		+	+

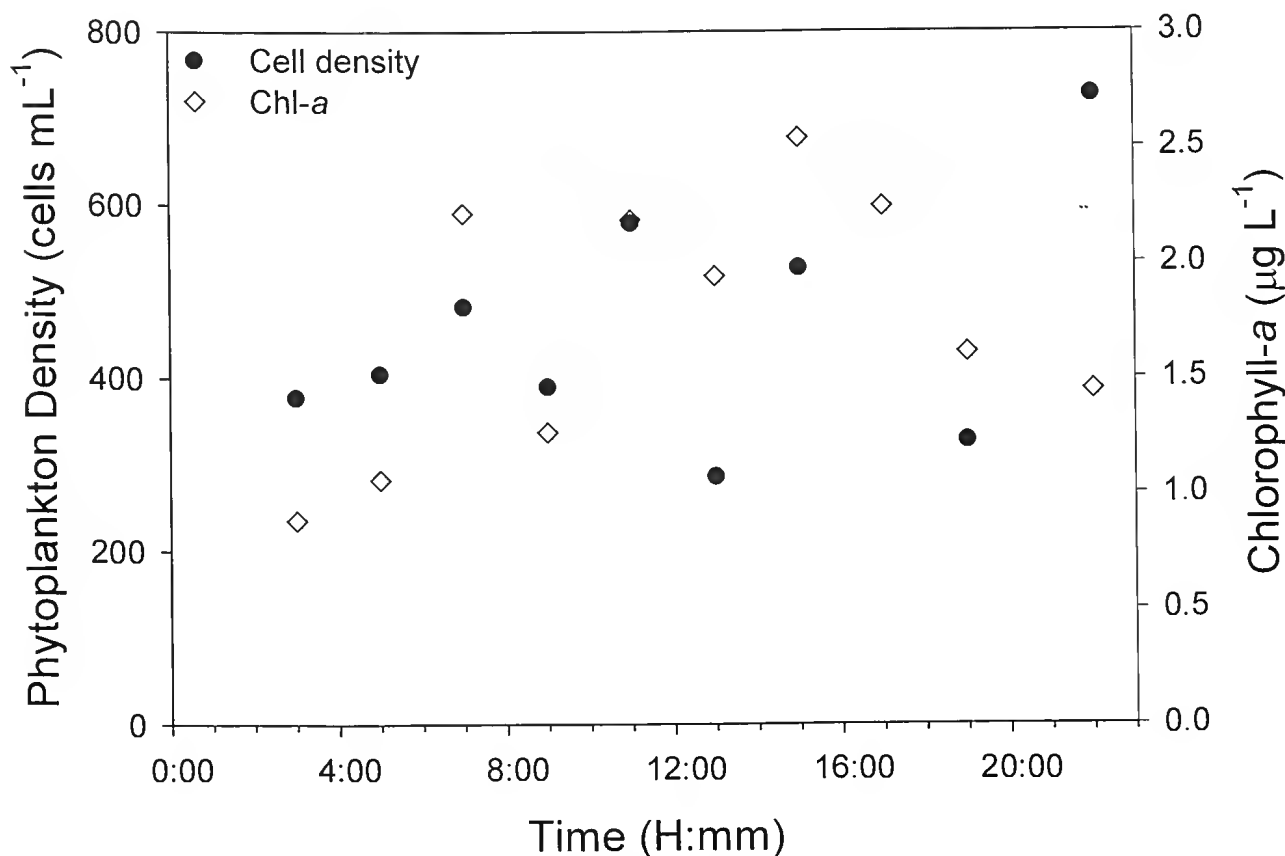


Figure 3. Phytoplankton cell density and chl-*a* concentration in Fremantle Harbour over the duration of the study period. Inconsistencies at 1300 hrs and 2200 hrs relate to changes in species composition.

Diurnal variability in photosynthesis

Analysis of F_v/F_m data revealed a typical diurnal cycle pattern (Figure 4a). F_v/F_m was quite high (~ 0.65) at 03:00 and 04:00, however immediately prior to dawn F_v/F_m increased to a value of 0.81 ± 0.01 (error = se, $n = 10$). This value was very close to theoretically maximal values of 0.83 (Magnusson 1997). A rapid decrease in F_v/F_m occurred over the early daylight hours and, throughout most of the day, values between 0.57 and 0.60 were observed. F_v/F_m dropped below this to values of 0.51 ± 0.02 at 09:00, 0.54 ± 0.01 at 13:00 and 0.51 ± 0.01 at 15:00. Each of these minima were associated with a period of high incident irradiance during the sample collection period (Figure 4a).

The maximum photosynthetic rates as measured by chl-fluorescence ($rETR_{max}$) indicate that photosynthetic processes were substantially down-regulated during the night (Figure 4b). Re-induction of these processes was rapid and possibly even predictive, since photosynthetic capability, as indicated by $rETR_{max}$, began to increase prior to dawn. This development of photosynthetic capacity was also reflected by the sudden and large increase in α (Figure 4c). $rETR_{max}$ reached a peak at 08:00 (408 ± 10.6 relative units, error = se, $n = 10$) before declining again as the first periods of high irradiance ($852 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ at 08:30; Figure 4a) resulted in downregulation of photosynthesis and potentially some photoinhibition. Downregulation was indicated by the earlier and

proportionately greater drop in α compared to $rETR_{max}$, leading to higher values for E_k (Figure 4d).

The depression of F_v/F_m at 09:00 and a concomitant decrease in $rETR_{max}$ and E_k , after a gap in the clouds resulted in the first period of high irradiance for the day (Figure 4), suggested photoinhibition due to damage of the photosynthetic apparatus may have occurred. A substantial recovery of F_v/F_m from 0.51 ± 0.02 (error = se) at 09:00 to 0.59 ± 0.01 in the following hour suggests that down-regulation rather than photoinhibition was responsible for the downturn in photosynthesis; however a continuing slow recovery of F_v/F_m over the next 2 hours of cloud cover (minima for this period was $318 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ at 10:50) indicates that some photodamage did occur. Depression of F_v/F_m was observed again at 13:00 and 15:00 after extended periods of high light, with the 15:00 depression being accompanied by decreases in $rETR_{max}$ and α despite slightly lower incident irradiances (Figure 4). By dusk $rETR_{max}$ began to decrease substantially despite large increases in photosynthetic efficiency (as indicated by α). This suggests substantial rate limitation by the Calvin-Benson cycle as its associated light activated enzymes begin to 'switch off'. The diurnal pattern of a closely reflected F_v/F_m changes, given that the initial slope is the product of the chl-specific absorption coefficient and maximum photosynthetic efficiency, this suggests that the light absorption characteristics remained relatively stable throughout the day.

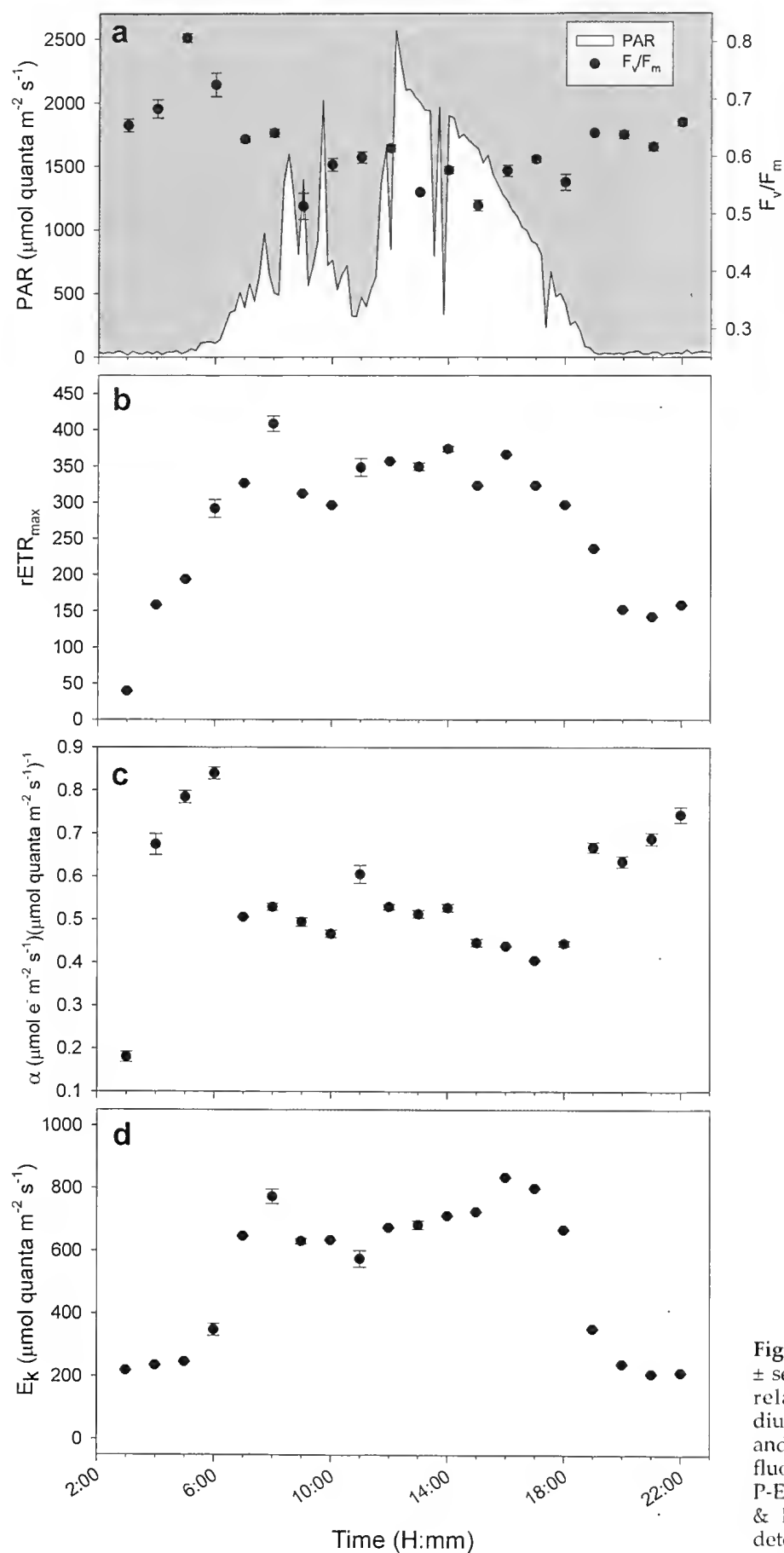


Figure 4. (a) Phytoplankton F_v/F_m (mean \pm se, $n = 10$) over the course of the day relative to incident irradiance. The diurnal changes in (b) $rETR_{\text{max}}$, (c) α and (d) E_k parameters measured by chl-*a* fluorescence as determined by modelling P-E curve data with the model of Eilers & Peeters (1988) (error bars = se as determined by the model).

DISCUSSION

The phytoplankton community in the coastal marine waters sampled at the mouth of the Swan-Canning Estuary (this study) was found to be dominated by members of the Bacillariophyceae (diatoms) (Figure 2, Table 1). Dominance of diatoms in both near-shore coastal waters (Thompson & Waite 2003) and in the lower reaches of the Swan-Canning Estuary (Thompson 1998) has been described previously. The persistent dominance of diatoms throughout the study was fortunate, as shifts in taxonomic composition between species with different pigments (light harvesting and accessory) and/or thylakoid arrangements can influence the signature obtained by PAM fluorometers (Büchel & Wilhelm 1993). Thus, the observed taxonomic stability gave some confidence to the assumption that changes in fluorescence signal represented changes in physiological state of the phytoplankton community rather than taxonomic shifts.

Chl-*a* concentrations ranged between 0.88 $\mu\text{g L}^{-1}$ at 03:00 to 2.54 $\mu\text{g L}^{-1}$ at 15:00 (Figure 3). Peaks in chl-*a* concentration above $\sim 1.6 \mu\text{g L}^{-1}$ were dependent on the presence of large, chlorophyll-rich diatom species such as *Chaetoceros curvictetus*, *Chaetoceros laciniosus* and *Skeletonema costatum*. The chl-*a* concentrations here were similar to those recorded at Blackwall Reach, about 6 km upstream, by Thompson (1998), although cell densities were substantially lower. Despite the Water-PAM's reported lower-limit of chl-*a* detection being 0.1 $\mu\text{g L}^{-1}$, the fluorescence signal was found to be unstable and sample concentration was required in order to achieve a stable and reliable fluorescence trace over the course of fluorescence measurements. Concentration of samples via the use of a plankton net may shock phytoplankton cells and can result in substantially lowered quantum yield measurements (Peter Ralph, pers. comm.). However, given that F_v/F_m values recorded after the concentration procedure were as high as 0.807 ± 0.007 (error = se, $n = 10$; Figure 4a), any negative impact on phytoplankton physiology was considered negligible.

Endogenous diel oscillations in the P-E response of marine phytoplankton have been widely reported (Boyd *et al.* 1997; Harding *et al.* 1981; Harding *et al.* 1982; Harris 1980) and diatoms appear to display greater diel periodicity than most other taxa (Behrenfeld *et al.* 2004; Harding *et al.* 1981). Studies have found maximum photosynthetic rate (P_{max}) to peak both in the morning (Marra *et al.* 1985) and afternoon (Harding *et al.* 1982). Timing differences in the pattern of diel changes have previously been explained by changes in latitudinal photoperiod and variations in nutrient assimilation and utilisation between phytoplankton size fractions (Harding *et al.* 1982). More generally, diel rhythms in P_{max} and α are commonly understood to result from oscillations between metabolic pathways which are influenced by light periodicity and exogenous nutrient supply (Harding *et al.* 1982; Behrenfeld *et al.* 2004). Nutrients accumulated during dark periods may help to yield a high P_{max} the following morning (Erga & Skjoldal 1990). Henley (1993) states that maximum photosynthetic rate usually peaks in the morning or close to midday and that this pattern may be endogenous, rather than related to chl-content, photoinhibition, nutrition or feedback inhibition by accumulated photosynthate. In this study,

the observed pattern in $rETR_{\text{max}}$ appear to be a response to the changing light environment; with increasing values in the morning as key Calvin-Benson cycle enzyme such as Ribulose-1,5-bisphosphate-carboxylase/oxygenase (RuBisCo) become activated at dawn ("light activation") (Buchanan 1980) and down-regulation or inhibition during the middle part of the day as RCIIIs become closed or damaged (Figure 4a, b). However, the significant increase in $rETR_{\text{max}}$ prior to dawn suggests that, to some extent, an endogenous rhythm was also present.

The PAM chl-fluorescence parameters F_v/F_m , $rETR_{\text{max}}$ and α indicate possible photoinhibition of phytoplankton photosynthesis at 09:00, 13:00 and 15:00 (Figure 4). Measurements at 09:00 were taken shortly after a break in cloud cover resulted in surface irradiances of $\sim 1500 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ and F_v/F_m was found to be depressed (0.51 ± 0.023 compared to 0.64 ± 0.007 at 08:00). This drop in F_v/F_m was accompanied by a lower recorded $rETR_{\text{max}}$, while α had undergone a sudden decrease at 07:00 and subsequently remained relatively stable. A common measure of photosynthetic efficiency and physiological stress, the chl-fluorescence parameter F_v/F_m is extensively used to describe diurnal patterns in photosynthesis. Diurnal variability in F_v/F_m has been shown to be closely related to incident irradiance and midday depression of F_v/F_m is frequently observed when irradiance is high (ie. no or limited cloud cover) (e.g. Bergmann *et al.* 2002). However, it should not be assumed that F_v/F_m maxima and minima always occur during the evening and around midday respectively. Behrenfeld and Kolber (1999) describe measurements taken in the South Pacific Ocean (prokaryote-dominated phytoplankton community in iron limited conditions) that exhibit nocturnal F_v/F_m minima. Reduction of F_v/F_m can result from a number of physiological processes including numerous pathways for down-regulation of photosynthesis and closure of photosystem II reaction centres (RCIIIs) due to photoinhibition associated with damage to the D1 protein within the core of photosystem II (Adams III *et al.* 2006; Cartaxana *et al.* 2013; Edelman & Mattoo 2006). Changes in chl-fluorescence can be used to make inferences about the photophysiological state of phytoplankton cells in the sample. A disproportionate reduction of F_0 compared to F_m may represent enhanced xanthophyll cycle activity (photoprotection) or enhanced NADPH-reductase activity leading to state transition and photosystem II being in state-2 in the dark (Demmig & Björkman 1987; Magnusson 1997; Fracheboud 2001); while a decline in F_m and increase in F_0 can indicate photoinhibition and closure of damaged reaction centres (Campbell *et al.* 2003; Franklin *et al.* 1992). The sampling methods undertaken did not allow for comparison of F_0 and F_m between sampling periods and thus achieving a more quantitative assessment of the proportion of photoinhibition compared to photoregulatory down-regulation was not possible. The low signal to noise ratio of the conducted PAM chl-fluorescence measurements meant that quenching parameters were considered inconclusive (data not shown).

The highest irradiances for the day were recorded between midday and 13:00 as cloud cover that had persisted for most of the morning dissipated (Figure 4a). The F_v/F_m of the phytoplankton community decreased

from 0.61 ± 0.007 at midday to 0.54 ± 0.005 at 13:00 (Figure 4a), however on this occasion there was no concomitant decrease in $rETR_{max}$ (Figure 4b). Data from Olaizola *et al.* (1994) suggest that changes in diadinoxanthin cycle pigment pool size could occur between hourly sampling periods. An increase in dissipative diatoxanthin content relative to chl-*a* would result in a decrease in both F_m and F_o (Lavaud *et al.* 2004), however F_v/F_m would also decrease as the drop in F_m is proportionately greater. It has been proposed that epoxidase activity is inhibited after exposure to high light (Olaizola *et al.* 1994). Thus the low F_v/F_m recorded during this study at 13:00 may be the result of diatoxanthin remaining de-epoxidized in the dark and increased levels of non-photochemical quenching rather than significant photodamage to RCII.

Similar to the pattern seen at 09:00, at 15:00 the drop in F_v/F_m was associated with a concomitant reduction of $rETR_{max}$ indicating that some photoinhibition may have occurred (Figure 4a, b). However, substantial recovery of F_v/F_m was observed within the hour after each decline, indicating that this was more likely to be an expression of dynamic regulatory mechanisms rather than photoinhibition (recovery from photoinhibition occurs on a time scale of hours to days).

Evidence of active quenching mechanisms was present in the pattern of E_k . Boyd *et al.* (1997) interpreted a significant decrease in E_k towards evening as relaxation of non-photochemical quenching. In this study, the substantially higher E_k values during the daylight hours compared to before dawn and after dusk (Figure 4d) resulted from a significant decline in α (Figure 4c) with little or no reduction in $rETR_{max}$ (Figure 4b) and can be construed as an increase in non-photochemical quenching. Also, the diurnal pattern of the P-E curve parameters tends to represent a photoacclimation response type A, as described by Richardson *et al.* (1983), where the activity of accessory pigments is thought to play a major role.

Diatoms, via the diadinoxanthin cycle, are capable of efficient downregulation of photosynthesis via non-radiative dissipation of excess energy (Cartaxana *et al.* 2013; Lavaud *et al.* 2002). The data presented here suggest that the diatom-dominated marine phytoplankton community found in Perth's coastal waters at the time of this study was capable of avoiding photoinhibitory damage by employing this tactic.

Along with the recorded high F_v/F_m values, the ability of the phytoplankton community to effectively regulate photosynthesis and avoid photodamage suggests that they were not nutrient limited. However, the nutrient concentrations of Perth's coastal waters have been described as "in the lower part of the range reported for temperate coastal waters elsewhere" (Johannes *et al.* 1994) with low N:P ratios resulting in a likelihood of N-limitation (Thompson & Hosja 1996). It is possible that phytoplankton at the mouth of the Swan-Canning Estuary at the time of this study were efficiently recycling nutrients from within the plankton community, or turbulence of the water column due water movement through the mouth of estuary provided sufficient nutrients via suspension of benthic solids however further studies would be needed to quantitatively

determine phytoplankton nutrient status and the source of these nutrients.

CONCLUSION

The marine phytoplankton community at the mouth of the Swan-Canning estuary exhibited a typical diurnal pattern of photosynthesis, with maximum rates of photosynthesis occurring during the daylight hours as photosynthetic processes became rapidly induced. Studies assessing the productivity of microalgae in the system would need to take such diurnal variations into account.

High F_v/F_m values, reaching close to the theoretical maximum just prior to dawn, suggested that phytoplankton were physiologically competent and not nutrient-limited. The fast recovery of F_v/F_m after periods of high light while maintaining near maximal rates of photosynthesis ($rETR_{max}$) supports this finding and highlights the photoprotective ability of diatoms, which were the dominant taxon.

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REFERENCES

- ADAMS III, W, ZARTER, R, MUEH, K E, AMIARD, V & DEMMIG-ADAMS, B 2006. Energy dissipation and photoinhibition: A continuum of photoprotection. In: Demmig-Adams, B, Adams III, W and Mattoo, A K (eds) *Photoprotection, photoinhibition, gene regulation, and environment*. Vol. 21. pp. 49–64. Springer, Dordrecht.
- BAKER, N R & OXBOROUGH, K 2004. Chlorophyll fluorescence as a probe of photosynthetic productivity. In: Papageorgiou, G and Govindjee (eds) *Chlorophyll a fluorescence: A signature of photosynthesis*. Vol. 19. pp. 65–82. Springer, Dordrecht.
- BEHRENFELD, M, PRASIL, O, BABIN, M & BRUYANT, F 2004. In search of a physiological basis for covariations in light-limited and light-saturated photosynthesis. *Journal of Phycology* 40, 4–25.
- BERGMANN, T, RICHARDSON, T L, PAERL, H W, PINCKNEY, J L & SCHOFIELD, O 2002. Synergy of light and nutrients on the photosynthetic efficiency of phytoplankton populations from the Neuse River estuary, North Carolina. *Journal of Plankton Research* 24, 923–933.
- BOYD, P, AIKEN, J & KOLBER, Z 1997. Comparison of radiocarbon and fluorescence-based (pump-and-probe) measurements of phytoplankton photosynthetic characteristics in the northeast Atlantic ocean. *Marine Ecology Progress Series* 149, 215–226.
- BUCHANAN, B B 1980. Role of light in the regulation of chloroplast enzymes. *Annual Review of Plant Physiology* 31, 341–374.
- BÜCHEL, C & WILHELM, C 1993. *In vivo* analysis of slow chlorophyll fluorescence induction kinetics in algae: Progress, problems and perspectives. *Photochemistry and Photobiology* 58, 137–148.
- CAMPBELL, S, MILLER, C, STEVEN, A & STEPHENS, A 2003. Photosynthetic responses of two temperate seagrasses across

- a water quality gradient using chlorophyll fluorescence. *Journal of Experimental Marine Biology and Ecology* 291, 57–78.
- CARTAXANA, P., DOMINQUES, N., CRUZ, S., JESUS, B., LAVIALE, M., SERODIO, J. & MARQUES DA SILVA, J. 2013. Photoinhibition in benthic diatoms assemblages under light stress. *Aquatic Microbial Ecology* 70, 87–92.
- COSGROVE, J. & BOROWITZKA, M. 2010. Chlorophyll fluorescence terminology: An introduction. In: Suggett, D. J., Prášil, O. and Borowitzka, M. A. (eds) *Chlorophyll a fluorescence in aquatic sciences: Methods and applications*. pp. 1–17. Springer, Dordrecht.
- DIJKMAN, N. A. & KROMKAMP, J. C. 2006. Photosynthetic characteristics of the phytoplankton in the scheldt estuary: Community and single-cell fluorescence measurements. *European Journal of Phycology* 41, 425–434.
- EDELMAN, M. & MATTOO, A. K. 2006. The d1 protein: Past and future perspectives. In: Demmig-Adams, B., Adams III, W. W. and Mattoo, A. K. (eds) *Photoprotection, photoinhibition, gene regulation, and environment*. Vol. 21. pp. 23–38. Springer, Dordrecht.
- EILERS, P. & PEETERS, J. 1988. A model for the relationship between light intensity and the rate of photosynthesis in phytoplankton. *Ecological Modelling* 42, 199–215.
- ERGA, S. R. & SKJOLDAL, H. R. 1990. Diel variations in photosynthetic activity of summer phytoplankton in lindåspollene, western Norway. *Marine Ecology Progress Series* 65, 73–85.
- FRANKLIN, L., LEVAVASSEUR, G., OSMOND, C. B., HENLEY, W. & RAMUS, J. 1992. Two components of onset and recovery during photoinhibition of *ulva rotundata*. *Planta* 186, 399–408.
- HAMILTON, D. P., DOUGLAS, G. B., ADENEY, J. A. & RADKE, L. C. 2006. Seasonal changes in major ions, nutrients and chlorophyll *a* at two sites in the Swan River estuary, Western Australia. *Marine and Freshwater Research* 57, 803–815.
- HARDING, L. W., JR., MEESON, B. W., PRÉZELIN, B. & SWEENEY, B. 1981. Diel periodicity of photosynthesis in marine phytoplankton. *Marine Biology* 61, 95–105.
- HARDING, L. W., JR., PRÉZELIN, B. B., SWEENEY, B. M. & COX, J. L. 1982. Diel oscillations of the photosynthesis-irradiance (p-i) relationship in natural assemblages of phytoplankton. *Marine Biology* 67, 167–178.
- HARRIS, G. P. 1980. The measurement of photosynthesis in natural populations of phytoplankton. In: Morris, I. (ed.) *Physiological ecology of phytoplankton*. pp. 129–187. University of California Press, Berkeley, CA.
- HENLEY, W. 1993. Measurement and interpretation of photosynthetic light-response curves in algae in the context of photoinhibition and diel changes. *Journal of Phycology* 29, 729–739.
- HILLMAN, K., MCCOMB, A. J. & WALKER, D. I. 1995. The distribution, biomass and primary production of the seagrass *halophila ovalis* in the Swan/Canning estuary, Western Australia. *Aquatic Botany* 51, 1–54.
- JEFFREY, S. W. & HUMPHREY, G. F. 1975. New spectrophotometric equations for determining chlorophylls *a*, *b*, *c₁*, and *c₂* in higher plants, algae, and natural phytoplankton. *Biochimie und Physiologie der Pflanzen* 167, 191–194.
- JOHANNES, R., PEARCE, A., WIEBE, W., CROSSLAND, C., RIMMER, D., SMITH, D. & MANNING, C. 1994. Nutrient characteristics of well-mixed coastal waters off Perth, Western Australia. *Estuarine, Coastal and Shelf Science* 39, 273–285.
- KURZBAUM, E., BEER, S. & ECKERT, W. 2010. Alterations in delayed and direct phytoplankton fluorescence in response to the diurnal light cycle. *Hydrobiologia* 639, 197–203.
- LAVAUD, J., ROUSSEAU, B. & ETIENNE, A.-L. 2004. General features of photoprotection by energy dissipation in planktonic diatoms (bacillariophyceae). *Journal of Phycology* 40, 130–137.
- LAVAUD, J., ROUSSEAU, B., VAN GORKOM, H. J. & ETIENNE, A.-L. 2002. Influence of the diadinoxanthin pool size on photoprotection in the marine planktonic diatom *plaeodactylum tricornutum*. *Plant Physiology* 129, 1398–1406.
- MACKAY, K. R. M., PAYTAN, A., GROSSMAN, A. R. & BAILEY, S. 2008. A photosynthetic strategy for coping in a high-light, low-nutrient environment. *Limnology and Oceanography* 53, 900–913.
- MAGNUSSON, G. 1997. Diurnal measurements of fv/fm used to improve productivity estimates in microalgae. *Marine Biology* 130, 203–208.
- MARRA, J., HEINEMANN, K. & LANDRIAU, G., JR. 1985. Observed and predicted measurements of photosynthesis in a phytoplankton culture exposed to natural irradiance. *Marine Ecology Progress Series* 24, 43–50.
- MASINI, R. J. & MCCOMB, A. J. 2001. Production by microphytobenthos in the Swan-Canning estuary. *Hydrological Processes* 15, 2519–2535.
- OLAIZOLA, M., LA ROCHE, J., KOLBER, Z. & FALKOWSKI, P. 1994. Non-photochemical quenching and the diadinoxanthin cycle in a marine diatom. *Photosynthesis Research* 41, 357–370.
- RICHARDSON, K., BEAROALL, J. & RAVEN, J. A. 1983. Adaptation of unicellular algae to irradiance: An analysis of strategies. *New Phytologist* 93, 157–191.
- STRICKLAND, J. D. H. & PARSONS, T. R. 1972. *A practical handbook of seawater analysis*. 2nd edn. Fisheries Research Board of Canada, Ottawa.
- THOMPSON, P. 1998. Spatial and temporal patterns of factors influencing phytoplankton in a salt wedge estuary, the Swan River, Western Australia. *Estuaries* 21, 801–817.
- THOMPSON, P. & HOSJA, W. 1996. Nutrient limitation of phytoplankton in the upper Swan River estuary, Western Australia. *Marine and Freshwater Research* 47, 659–667.
- THOMPSON, P. & WAITE, A. 2003. Phytoplankton responses to wastewater discharges at two sites in Western Australia. *Marine and Freshwater Research* 54, 721–735.
- THOMPSON, P. A. 2001. Temporal variability of phytoplankton in a salt wedge estuary, the Swan-Canning estuary, Western Australia. *Hydrological Processes* 15, 2617–2630.
- TOMAS, C. R. (Ed.) 1997. *Identifying marine phytoplankton*. Academic Press, San Diego.
- TWOMEY, L. J. & JOHN, J. 2001. Effects of rainfall and salt-wedge movement on phytoplankton succession in the Swan-Canning estuary, Western Australia. *Hydrological Processes* 15, 2655–2669.
- VERSPECHT, F. 2007. *Temporal dynamics of the coastal water column*. Ph.D. Thesis, University of Western Australia, Perth.
- ZHANG, M., KONG, F., WU, X. & XING, P. 2008. Different photochemical responses of phytoplankters from the large shallow taihu lake of subtropical China in relation to light and mixing. *Hydrobiologia* 603, 267–278.

Recovery of seabird colonies on Rat Island (Houtman Abrolhos) following the eradication of introduced predators

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The large seabird colonies on Rat Island in the Houtman Abrolhos group were extirpated by the combined impacts of introduced *Rattus rattus* (black rat) and *Felis catus* (cat) as well as guano mining by the 1930s. Both introduced predators were eradicated following a baiting program conducted in 1991, with the last cat dying around 2000. The Rat Island Recovery Project was established to monitor the return of breeding seabirds after an absence of approximately 60 years. The seabird colonies began to re-establish within a decade of the eradication program and the number of species and breeding pairs on Rat Island increased dramatically in 2011 and 2012. The recovery of the seabird colonies presents a number of management issues on an island where human uses have developed in their absence. Management decisions will also need to be made about whether to enhance the recovery of important natural processes by facilitating the restoration of some of the conservation values lost from the terrestrial ecosystem on Rat Island.

KEYWORDS: eradication, introduced predators, islands, recovery, restoration, seabird colonies

INTRODUCTION

The eradication of introduced predators from islands is now a widely practiced conservation measure (Veitch *et al.* 2011; Dunlevy *et al.* 2011). However, the long time intervals between treatment and response have made it difficult for managers to find resources to monitor and record subsequent ecological trajectories or apply adaptive management approaches to enhancing restoration outcomes.

The eradication of black rats and feral cats from Rat Island in Western Australia is predicted to be the initial critical intervention in the recovery of the terrestrial ecosystem by providing for the return of breeding seabirds and the associated marine nutrient subsidy (Smith *et al.* 2011). The marine nutrient and energy resources, transferred by seabirds from sea to land, are expected to drive the partial recovery of the terrestrial ecosystem by rebuilding soil organic matter, increasing primary productivity and providing for scavengers (Mulder *et al.* 2011). Changes in the flora might also be predicted with the increased nutrient availability favouring faster-growing species including regional nitrophilous and ornithocoprophilic plants. Invertebrate and reptile populations are likely to increase in abundance in response to the increased primary productivity, and more species from the regional pool of volant insects and birds may be able to colonise and increase the islands biodiversity (Mulder *et al.* 2011).

RAT ISLAND

Rat Island is an elevated (3–4 m above MSL) relatively flat island in the Easter Group of the Houtman Abrolhos archipelago 78 km west of Geraldton, Western Australia (Figure 1). The island is broadly rectangular in shape

with its long axis oriented north–south, and is comprised of coralline limestone (Wallabi Limestone) formed during the highstand of the Eemian stage 125 000 years BP (Collins *et al.* 1997). It has a supratidal area of 61 ha and is sparsely vegetated (Harvey *et al.* 2001). The area would have been a low coastal ridge during the latter part of the Pleistocene and then isolated from the mainland by the most recent marine transgression about 7000 years ago. Colonisation by seabirds and the accumulation of its historical mantle of guano would have occurred during the later Holocene period.

The Abrolhos archipelago is perched on the edge of the continental shelf, adjacent to the southward-flowing Leeuwin Current, and consequently provides important breeding sites for seabirds, particularly tropical species (Storr *et al.* 1986; Gaughan *et al.* 2002).

Guano mining began in earnest on Rat Island in 1885 and wound up in 1915 (Stanbury 1993; Burbidge *et al.* 1996). The predominately Chinese mine workers dug and swept up the guano-enriched soil, levering out the surface limestone in order to get access to the material sequestered in fissures and cracks. Low embankments were constructed for trolley lines that carried the excavated material back to the shipping stockpiles at the northeastern end of the Island. The product was then loaded onto vessels via trolley lines that ran out onto a stone jetty.

The habitat available to nesting seabirds was drastically altered during this time. The soil was almost completely removed from about 81% of the island's surface, leaving limestone pavement, sink holes, rock-piles of coralline slabs, piles of smaller diameter screened rock material, a system of anastomosing low embankments and little perennial woody vegetation (Dunlop & Rippey 2004).

The eastern edge of Rat Island provides sheltered access to deep water and has provided suitable sites for

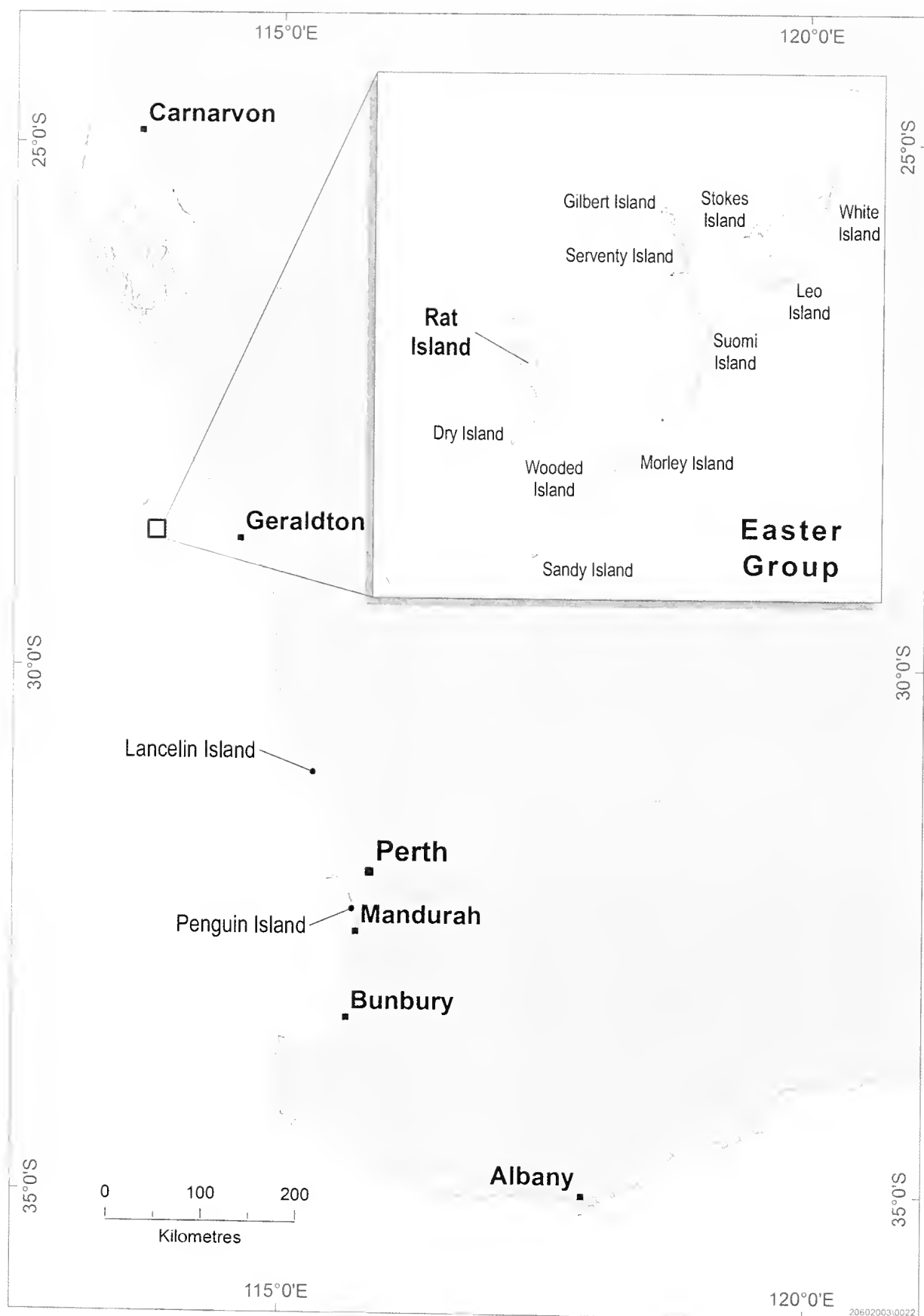


Figure 1. Location map of Rat Island in the Easter Group of the Houtman Abrolhos Islands off Geraldton in southwestern Australia.

fishing camps since at least the 1940s. Since World War II professional *Panulirus cygnus* (western rock lobster) fishers have occupied these camps. There have been up to 59 rock lobster camps on Rat Island (currently over 70 shacks) and one camp associated with the operations of a cultured-pearl lease. The foundations of a number of abandoned camps occur to the south of the current settled area. The settlement footprint of Rat Island, including an airstrip and access pathways, is ~14 ha or 22.9% of the total area (Rat Island Recovery Project, unpubl. data). However, much of this area was formerly mined for guano and would have little additional impact on the island's biodiversity.

In 2004 the Rat Island Recovery Project was established and began with a feasibility study published in January of that year and provided to the Department of Fisheries (Dunlop & Rippey 2004). Since 2008 the project has sought to monitor and document the recovery of the Rat Island seabird colonies and the terrestrial ecosystem following the successful eradication of black rats and feral cats in the 1990s and to facilitate restoration projects that may enhance the recovery process. The timing of the Rat Island Recovery Project (2003–2013) has provided a unique opportunity to investigate and document seabird responses to a successful introduced predator eradication program conducted during the 1990s. This paper documents the early trends in the recovery of Rat Island's seabird colonies. The next phase in the Rat Island Recovery Project will focus on the recovery of the island's terrestrial ecosystem following seabird recolonisation.

History of seabird colonies

Rat Island was surveyed and named by Lieutenant John Lort Stokes on the HMS *Beagle* in April 1840. Evidently the island was already populated with black rats to the extent that they gave its name: '*The centre island we named Rat Island, from the quantity of that vermin with which it was infested.*' (Stokes 1846 p. 145).

The presence of black rats prior to any European inhabitation of the Abrolhos is puzzling but was presumably the result of some undocumented visit by a sailing ship or of a shipwreck. Stokes visited in April (Stokes 1846), a period outside the spring–summer breeding period of the large colonies of tropical terns on Rat Island. These colonies were documented later in the colonial period.

Rat Island was the scene of what has become arguably the best-documented ecological calamity in the history of European settlement in Western Australia. Archibald James Campbell estimated in 1889 that the mixed colony of *Anous stolidus* (common noddy) and *Sterna fuscata* (sooty tern) held 1 452 000 birds (Serventy *et al.* 1971). These colonies were completely extirpated by the late 1930s through the combined effects of guano mining, the introduction of cats, and egg collecting by fishermen (Burbidge *et al.* 1996).

During the colonial period the Rat Island tern colonies were at least three times the size of the spectacular breeding aggregations that still occur on the southern end of Pelsaert Island (Burbidge *et al.* 1996) in the Southern Group. Gibson (1908) visited both islands and noted that the sooty tern colony on Rat Island was much

larger than the one on Pelsaert. His observations effectively confirm that the colonies on Pelsaert Island today are not the result of displacement from the Rat Island population.

As well as the spectacular tern colonies, Rat Island had thousands of *Puffinus pacificus* (wedge-tailed shearwater) burrows in its guano mantle and low sand dunes until at least 1913 (Stanbury 1993; Alexander 1922). Other Abrolhos seabird species may also have nested on Rat Island at the time, particularly those (of larger size) that were least vulnerable to rat predation.

By the time the rock lobster fishing settlement became established at the Abrolhos in the 1950s Rat Island was a worked-out exhausted environment, now silent with the loss of its great tern and shearwater colonies. Many surface-nesting seabirds such as terns could potentially have utilised the mined-out landscape for breeding in the absence of the introduced predators. However, the thorough removal of the guano mantle and overlying low sand dunes effectively eliminated the nesting habitat for burrowing species (shearwaters and storm-petrels) over much of the surface.

Impact of introduced predators

Despite the presence of black rats, the constant disturbance of the guano diggers and dramatic changes in nesting habitat, the tern colonies on Rat Island were still reported to be 'prodigious' in November 1913 (Alexander 1922). Some eggging by fishermen is thought to have occurred both during and after the guano mining years, but this was unlikely to have been beyond sustainable levels as the Sooty Tern is quite tolerant of egg harvesting (Ridley & Percy 1958). However cats, introduced by the guano miners between 1889 and 1913 (Alexander 1922) to control the rats, became established and preyed on nesting terns during the breeding season. Alexander (1922) predicted the extirpation of the common noddies in the Rat Island colony after observing the impact of cat predation during his visit in 1913.

A small and dwindling number of common noddies were still present on Rat Island in 1936 and sooty terns were still present in 1938, but both species were probably extirpated around that time (Burbidge *et al.* 1996). *Egernia stokesii stokesii* (spiny-tailed skink, a subspecies endemic to the Abrolhos Islands) occurred on Rat Island. It also appears to have been extirpated from Rat Island by the cats.

The process that occurred on Rat Island appears to be an example of 'hyperpredation' (Russell & Le Corre 2009; Russell 2011) caused by the interaction of two introduced predators, in this case the black rat and the cat. High concentrations of seabirds were persisting in the presence of the black rats until the introduction of cats by the guano miners. These seabirds (mainly sooty terns and common noddies) had a limited, highly synchronised breeding season and it is suggested that they were able to 'swamp' the rats with their enormous numbers over a short period of time. As indicated by Alexander (1922) the prey availability for cats outside this season was limited. This low food abundance on Rat Island during the autumn and winter may have reduced rat numbers to relatively low levels at the start of spring and the onset of seabird breeding. However, as with other examples of

hyperpredation (Russell 2011), cats could switch from seabird to rat and rabbit (also historically present on Rat Island) consumption in autumn and winter and consequently maintain their numbers between seabird breeding seasons. The depredations from the relatively high cat populations during the breeding seasons would then have been sufficient to drive rapid decline in the noddy and tern colonies on Rat Island. As the seabirds declined cat predation on the rats increased and both predator populations would probably have reduced to lower levels.

METHODS

Eradication of introduced predators

In 1991 Andrew Burbidge and Phil Fuller of the Department of Conservation and Land Management (Western Australia), Randall Owens from the Department of Fisheries (Western Australia) and Ken Johnson from the Conservation Commission (Northern Territory) undertook a program to eradicate black rats and cats from Rat Island. At the time there had been no confirmation of the presence of *Mus musculus* (house mouse). The objective of this intervention was primarily to prevent the black rat population on Rat Island and its satellites from becoming a platform for the invasion of other islands in the Easter Group and ultimately the rest of the Houtman Abrolhos, ie it was conceived as a biosecurity rather than an ecosystem recovery measure.

Rat Island and its near neighbours (Bushby, Little Rat, Roma, Little Roma and Dry) were baited with oats vacuum-impregnated with the anticoagulant rodenticide pindone. White Bank, just north of Rat Island, was inspected for rat sign, but no sign was found and it was not baited.

Baiting commenced on 30 November and was completed on 7 December 1991. About one cupful of bait was placed into thin plastic bags, which were placed on the ground, in a 50 m grid on the larger islands, and more densely spaced on smaller islands. Baits were inspected every three to four days and replaced if partially or completely consumed. All partly consumed bait bags were replaced with full bags at the end of the project and an additional bag of bait was placed in the centre of each 50 x 50 m grid at project completion.

Cat control using traps was conducted for several months after the rat baiting. No rats were observed after the baiting program was completed but one or two cats persisted for some years. The last surviving cat died in around 2000 (Russell Dyson pers. comm. 2003).

Seabird survey

The current investigation commenced with a field visit to Rat Island in December 2003. Observers made systematic day and night searches for breeding seabirds on each of the field surveys conducted in December 2003, December 2008, February 2012, August 2012, December 2012, February 2013 and April 2013. The number of breeding pairs was censused by locating and counting nest sites, counts of birds flying over colonies, or by mapping

colony boundaries and transect-based density sampling. The size of the large sooty tern colony in December 2012 was estimated by mapping the colony boundaries using GIS techniques and then estimating nest densities with seven randomly located 50 x 2 m (100 m²) belt transects. These transects were completed with head-torches at night when birds tended to remain incubating on the nest in the presence of the observers.

Adult and fledgling *Onychoprion anaethetus* (bridled terns) and sooty terns were individually marked with numbered alloy bands (supplied by the Australian Bird and Bat Banding Scheme) to enable future estimates of site and area fidelity in the adults and colony philopatry in the progeny reared on Rat Island.

RESULTS

Seabird recolonisation

RECORDS OF SEABIRD COLONIES PRIOR TO 2003

There were a number of records of incipient seabird recolonisation prior to that time. One pair of *Larus pacificus* (Pacific gull) was recorded breeding on Rat Island in 1996 and two pairs in 1999 (A A Burbidge pers. obs.). Twenty-one *Sternula nereis* (fairy tern) nests were counted on the beach at the northern end of Rat Island in November 1999 (A A Burbidge pers. obs.).

SEABIRD RECOLONISATION AFTER 2003

Surman & Nicholson (2009) reported six pairs of Pacific gulls and eight possible little shearwater burrows in December 2006 (outside the breeding season for the latter species). Our surveys in August suggested that not all of the Pacific gull pairs present in summer breed on Rat Island. We were also unable to confirm the presence of breeding *Puffinus assimilis* (little shearwater) during the breeding period (April and August).

About 300 pairs of fairy terns nested on Rat Island in November 2007 (R E Johnstone pers. comm. 2013).

The numbers of seabirds recorded breeding on Rat Island since 2003 are presented in Table 1. Since 2003 a considerable increase has been observed in both the number and diversity of seabirds nesting on the island.

Figure 2 represents the spatial extent of the colonies prior to 2012, and Figure 3 shows the colonies documented by the 2012–2013 breeding season. By 2012 (12 years after the demise of the last cat) eight seabird species had returned to breed on Rat Island. In 2012–2013 this involved an estimated 72 923 breeding pairs with the vast majority being sooty terns.

During December 2012 observers checked most of the other Easter Group islands known to have contained sooty tern colonies in recent years (Burbidge *et al.* 1996; C A Surman pers. comm. 2013; J N Dunlop pers. obs.: including Wooded, Morley, Leo, Campbell, Suomi, Keru, Serventy, Alexander and Gilbert Islands). All these islands were vacant suggesting that the entire Easter Group sooty tern breeding population had moved onto Rat Island in that year.

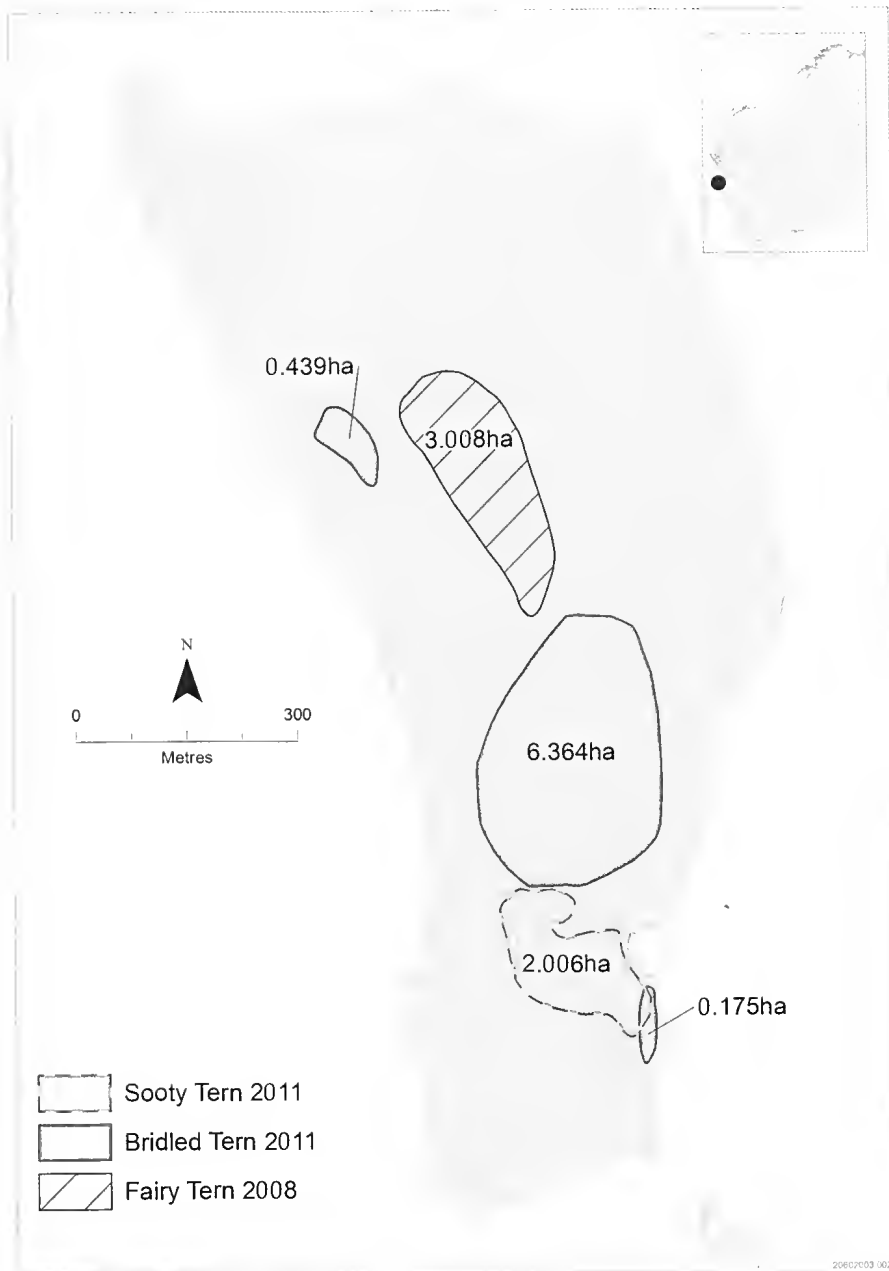


Figure 2. Seabird colonies up to the 2011–2012 season.

DISCUSSION

Seabird recolonisation trends

The earliest tentative indications of seabird recolonisation were observed in 1996, five years after rat eradication when there were one or two cats remaining on the island. Fairy terns (a species with little breeding site fidelity) established colonies in 1999, 2007 and 2008, with increasing colony size each year. Fairy terns naturally nest in the open on beaches, coral rubble or other reflective substrates with a preference for sites that provide nearby cover for chicks. The denuded, mined-out limestone surfaces (with nearby rock-piles) on Rat Island would appear to be ideal habitat for this species as a very large colony of 750 pairs was nesting there in December 2008 (Figure 2; Table 1).

When this project commenced in 2003 there were six breeding pairs of bridled terns nesting near the southern

end of the Island (Figure 2; Table 1). By 2008 there were between 50 and 100 pairs breeding at the southern end of the Island most with nests under rock-piles left by the guano miners. The early occurrence of the bridled tern is significant. Firstly as the regional metapopulation of this species has been rapidly expanding in response to changes in ocean climate (Dunlop 2011; Dunlop & Surman 2012) potentially increasing the number of prospectors around Rat Island. Secondly bridled terns prefer to nest under cover (provided in this case by the mined rock-piles), have high nest-site fidelity (eg on Penguin Island: Dunlop & Rippey 2005) and are a common nesting associate with other dark terns, including sooty terns in the Abrolhos and at Lancelin Island (Dunlop & Rippey 2004) (Figure 1). As such, the consistent presence of breeding bridled terns on Rat Island from 2003 to 2011 may have facilitated sooty tern settlement by breaking down the ‘information barrier’ with respect to colony predator security (Dunlop 2009).

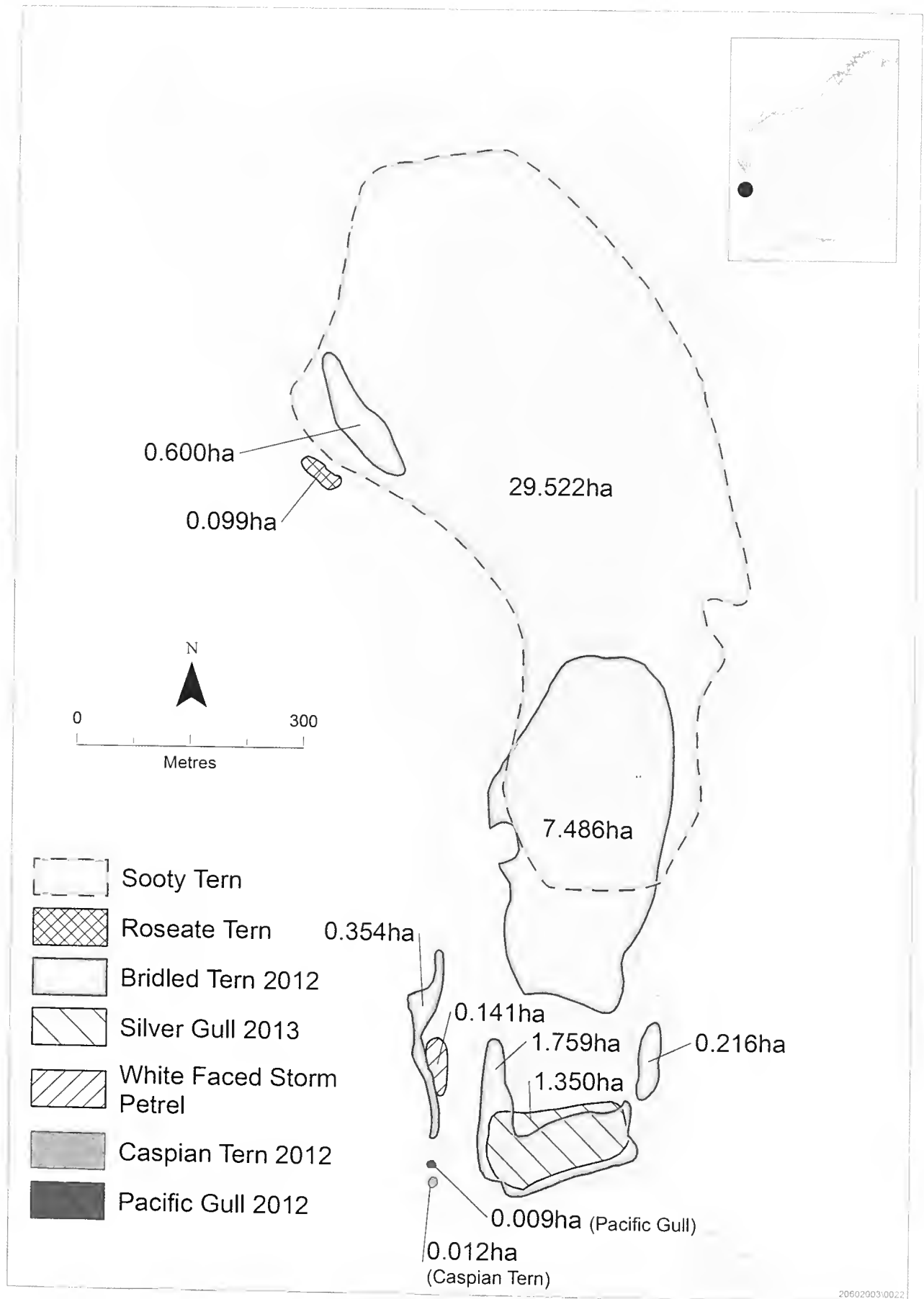


Figure 3. Seabird colonies in the 2012–2013 season.

Table 1. Rat Island Recovery Project records of breeding seabird numbers, colony areas and estimated colony densities on Rat Island from 2003 to 2013.

Seabird species	Date estimated	Area occupied (ha)	Estimated density (pairs/ha)	Colony size (pairs on Rat Island)
Bridled tern 2003	Dec 2003	–	–	6
Bridled tern 2008	Dec 2008	–	–	50–100
Bridled tern 2011	Feb 2012	6.9	25	174
Bridled tern 2012	Dec 2012	8.4	25	210
Fairy tern 2008	Dec 2008	3.0	–	750
Sooty tern 2011	Feb 2012	2.0	–	5000
Sooty tern 2012	Dec 2012	29.52	2400	72324
Roseate tern	Dec 2012	0.09	–	300
White-faced storm-petrel 2012	Aug 2012	0.14	51	27
Caspian tern 2012	Aug & Dec 2012	–	–	1
Pacific gull 2012	Dec 2012	–	–	1
Silver gull	Apr 2013	1.35	44	60

The initial sooty tern colony in 2010–2011 utilised remnant *Nitraria* and *Tecticornia* succulent heath at the southern island. This was expected as this is the breeding habitat utilised elsewhere in the Abrolhos (Serventy *et al.* 1971; Dunlop & Rippey 2004). However, the large colony in 2012 (Figure 3) utilised the guano-mined rock-pile habitats. Clearly in the absence of the introduced predators the existence of a novel habitat structure was not a significant barrier to sooty tern recolonisation.

The establishment of a colony of *Pelagodroma marina* (white-faced storm-petrel), sometime after 2008, was particularly remarkable as these small, burrow-nesting seabirds are particularly vulnerable to black rat and even house mouse predation and would not have been able to persist on Rat Island even prior to the introduction of the cats (Towns *et al.* 2011).

CONCLUSIONS

The monitoring of seabird responses to the eradication of introduced predators on Rat Island indicates that the initiation of seabird recolonisation can take place within a decade if there are drivers within regional metapopulations and a mechanism for overcoming the ‘information barrier’. Similar rates of recovery have been recorded on other seabird islands (Jones *et al.* 2011).

Even highly altered or novel habitats, such as mined-out guano fields, may be utilised by some surface-nesting seabird species in the absence of introduced predators. However, the recovery of seabird colonies after lengthy periods of absence may raise a range of management issues where various human uses and activities have become entrenched.

Terrestrial ecological recovery could, however, be limited or potentially derailed by some unremediated human-induced changes to Rat Island, including the removal of much of the soil by guano mining, introduced plants and animals, habitat degradation, human disturbance and the extent of the settlement footprint.

Future objectives for the management of Rat Island could settle for accommodating the changes now being

driven by the resumption of natural processes (recovery) or they could specify further interventions towards ecological restoration (Clewett & Aronson 2013). That is, taking actions intended to return the biodiversity of Rat Island closer to its original undisturbed condition. These interventions might include the control of some potential ecological weeds, the eradication of the house mouse population, the restoration of some habitat areas with remnant soil for burrow-nesting seabird species and the reintroduction of the extirpated reptiles.

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REFERENCES

- ALEXANDER W B 1922. The vertebrate fauna of Houtman's Abrolhos (Abrolhos Islands), Western Australia. *Journal of the Linnean Society (Zoology)* 34, 457–486.
- BURBIDGE A A, JOHNSTONE R E & FULLER P J 1996. The status of seabirds in Western Australia. In: Ross G J B, Weaver K & Greig J C (eds) *The status of Australia's seabirds*, pp. 57–71. Proceedings of the National Seabird Workshop, Canberra, 1–2 November 1993. Biodiversity Group, Environment Australia, Canberra.
- CLEWETT A F & ARONSON J 2013. *Ecological restoration. Principles, values, and structure of an emerging profession* (2nd edition). Island Press, Washington.

- COLLINS L B, ZHU Z R & WYRWOL K-H 1997. *Geology of the Abrolhos Islands*. In: Vacher L & Quinn T (eds) *Geology and hydrogeology of carbonate islands*, pp. 811–833. Elsevier, Amsterdam.
- DUNLEVY P, EBBERT S E, RUSSELL J C & TOWNS D R 2011. Eradication of invasive seabird predators on seabird islands. In: Mulder P H, Anderson W B, Towns D R & Bellingham P J (eds) *Seabird islands: ecology, invasion and restoration*, pp. 283–316. Oxford University Press, Oxford.
- DUNLOP J N 2009. The population dynamics of tropical seabirds establishing frontier colonies on islands of south-western Australia. *Marine Ornithology* 37, 99–106.
- DUNLOP J N 2011. Comparative foraging ecology in the dark tern guild breeding off south-western Australia—insights from stable isotope analysis. *Marine Ornithology* 39, 201–206.
- DUNLOP J N & RIPPEY E 2004. *Rat Island recovery project. A feasibility study*. Conservation Council (WA) for the Department of Fisheries, Western Australia.
- DUNLOP J N & RIPPEY E 2005. *The natural history of the bridled tern on Penguin Island, Western Australia*. Naragbup, Rockingham Regional Environment Centre.
- DUNLOP J N & SURMAN C A 2012. The role of foraging ecology in the contrasting responses two dark terns to a changing ocean climate. *Marine Ornithology* 40, 105–110.
- GAUGHAN D, SURMAN C, MORAN M, BURBIDGE A & WOOLLER R D 2002. Feeding ecology of seabirds nesting at the Abrolhos Islands, Western Australia. *Fisheries Research and Development Corporation Report* 1998/203.
- GIBSON C G 1908. Notes on some birds of the Abrolhos Islands (WA). *Emu* 8, 64–66.
- HARVEY J M, ALFORD J J, LONGMAN V M & KEIGHERY G 2001. A flora and vegetation survey of the Houtman Abrolhos, Western Australia. *CALMScience* 3, 521–623.
- JONES H P, TOWNS D R, BODEY T, MISKELLY C, ELLIS J C, RAUZON M, KRESS S & MCKOWN M 2011. Recovery and restoration on seabird islands. In: Mulder P H, Anderson W B, Towns D R & Bellingham P J (eds) *Seabird islands: ecology, invasion and restoration*, pp. 317–357 Oxford University Press, Oxford.
- MULDER P H, ANDERSON W B, TOWNS D R & BELLINGHAM P J (eds) 2011. *Seabird islands: ecology, invasion and restoration*. Oxford University Press, Oxford.
- RIDLEY M W & PERCY R 1958. Exploitation of seabirds in the Seychelles. *Colonial Research Studies* 25, 1–78.
- RUSSELL J C 2011. Indirect effects of introduced predators on seabird islands. In: Mulder P H, Anderson W B, Towns D R & Bellingham P J (eds) *Seabird islands: ecology, invasion and restoration*, pp. 261–279 Oxford University Press, Oxford.
- RUSSELL J C & LE CORRE M 2009. Introduced mammal impacts on seabirds in the Iles Eparses, Western Indian Ocean. *Marine Ornithology* 37, 121–129.
- SERVENTY D L, SERVENTY V & WARRIAM J 1971. *The handbook of Australian seabirds*. A H & A W Reed, Sydney.
- SMITH J L, MULDER C P H & ELLIS J C 2011. Seabirds as ecosystem engineers: nutrient inputs and physical disturbance. In: Mulder P H, Anderson W B, Towns D R & Bellingham P J (eds) *Seabird islands: ecology, invasion and restoration*, pp. 25–55 Oxford University Press, Oxford.
- STANBURY M 1993. Historic sites of the Easter Group, Houtman Abrolhos, WA. *Department of Maritime Archaeology, Western Australian Maritime Museum Report* 66.
- STOKES J L 1846. *Discoveries in Australia Volume 2*. Australiana Facsimile Edition No. 33. Libraries Board of South Australia.
- STORR G M, JOHNSTONE R E & GRIFFEN P 1986. Birds of the Houtman Abrolhos, Western Australia. *Records of the Western Australian Museum Supplement* 24, 1–42.
- SURMAN C A & NICHOLSON L W. 2009. A survey of the breeding seabirds and migratory shorebirds of the Houtman Abrolhos, Western Australia. *Corella* 33, 81–98.
- TOWNS D R, BYRD G V, JONES H R, RAUZON M J, RUSSELL J C & WHILCOX C 2011. Impacts of introduced predators on seabirds. In: Mulder P H, Anderson W B, Towns D R & Bellingham P J (eds) *Seabird islands: ecology, invasion and restoration*, pp. 56–90 Oxford University Press, Oxford.
- VEITCH C R, CLOUT M N & TOWNS D R (eds) 2011. *Island invasives: eradication and management*. Proceedings of the International Conference on Island Invasives. IUCN, Gland, Switzerland and Auckland, New Zealand.

Diet of feral cats, *Felis catus*, on Dirk Hartog Island

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ABSTRACT

Ten mammal species of conservation priority have been lost from Dirk Hartog Island, off the coast of Western Australia, most likely due to predation by the feral cat. We examined the diet of fourteen feral cats from Dirk Hartog Island to understand the potential impact of cat predation on remaining extant species. We examined the contents of the stomach and large intestine, and used stable isotope analysis of faeces, liver and muscle. The vertebrate species identified in the digestive tracts included at least six bird species, including two terrestrial birds and four shorebirds, seven reptile species, and one mammal (introduced *Mus musculus*). Analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ determined that the diet of feral cats was primarily terrestrially derived, although samples from the northern area of Dirk Hartog Island showed a skew towards marine derived food sources. The research findings showed that on this island, in the absence of rabbits, cats preyed mainly on terrestrial birds and reptiles.

KEYWORDS: Feral cat, diet, Dirk Hartog Island, stomach content and faecal analysis, stable isotopes

INTRODUCTION

Feral cats (*Felis catus*) are found on most major island groups worldwide (Nogales *et al.* 2004) and are thought to be the cause of extinctions of many native species, especially rodents (Fitzgerald 1988; Berovides & Comas 1991; Nowak 1999), reptiles (Iverson 1978; Gibbons 1984; Alberts 2000; Mitchell *et al.* 2002) and birds (Fuller 2000). On Dirk Hartog Island, off the coast of Western Australia, ten mammals have become locally extinct, of an original thirteen species recorded there (Baynes 1990; McKenzie *et al.* 2000; Algar *et al.* 2011; Table 1). The loss of these ten species from the island is most likely due to predation by the feral cat (Burbidge 2001; Burbidge & Manly 2002) and a cat eradication program is currently underway. If successful, Dirk Hartog Island will be the largest island worldwide to have feral cats eradicated. There is a plan to use Dirk Hartog Island as a site for fauna reconstruction and it could potentially support one of the most diverse mammal assemblages in Australia (Algar *et al.* 2011).

As part of the research program conducted prior to commencement of the feral cat eradication on Dirk Hartog Island, we examined the diet of cats in late autumn – the same time of year as that proposed for the baiting program, the primary control technique to be used. This study was expected to provide useful information on what cats were feeding on at that time of year and the potential impact on the effectiveness of the baiting program. The study also presented a unique opportunity to examine the diet of cats in the absence of introduced prey species, such as the rabbit (*Oryctolagus cuniculus*) and black rat (*Rattus rattus*), and in the absence of other introduced predators, such as the fox (*Vulpes*

vulpes). The house mouse (*Mus musculus*) is present on Dirk Hartog Island and, depending upon abundance, could contribute significantly to the feral cats' diet.

Stable isotope analysis can be used to overcome the limitations of the traditional diet analysis of faecal and stomach content (Stapp 2002) and it allows a larger dietary scope to be analysed as it is an integrated measure of different food sources over time, whereas analysis of stomach or faecal contents reveals only the last few meals. Carbon and nitrogen stable isotopes have been the most widely used for the identification of diet sources (Peterson & Fry 1987; Gannes *et al.* 1998; Hobson 1999; Kelly 2000; Stapp *et al.* 1999; Stapp 2002). This is attributed to the ability to determine foraging locations, particularly in coastal habitats, using carbon isotope ratios due to differences in pelagic and benthic food webs

Table 1. Extant and locally extinct mammals of Dirk Hartog Island (from Algar *et al.* 2011). * Introduced.

	Species	Common name
Extant	<i>Pseudomys albocinereus</i>	Ash-grey mouse
	<i>Pseudomys hermannsburgensis</i>	Sandy inland mouse
	<i>Sminthopsis dolichura</i>	Little long-tailed dunnart
	<i>Mus musculus</i>	House mouse*
Locally extinct	<i>Bettongia lesueur</i>	Boodie
	<i>Bettongia penicillata</i>	Woylie
	<i>Perameles bougainville</i>	Western barred bandicoot
	<i>Dasyurus geoffroii</i>	Chuditch
	<i>Dasyurus cristicaudata</i>	Mulgara
	<i>Parantechinus apicalis</i>	Dibbler
	<i>Leporillus conditor</i>	Greater stick-nest rat
	<i>Pseudomys desertor</i>	Desert mouse
	<i>Pseudomys fieldi</i>	Shark Bay mouse
	<i>Pseudomys shortridgei</i>	Heath mouse

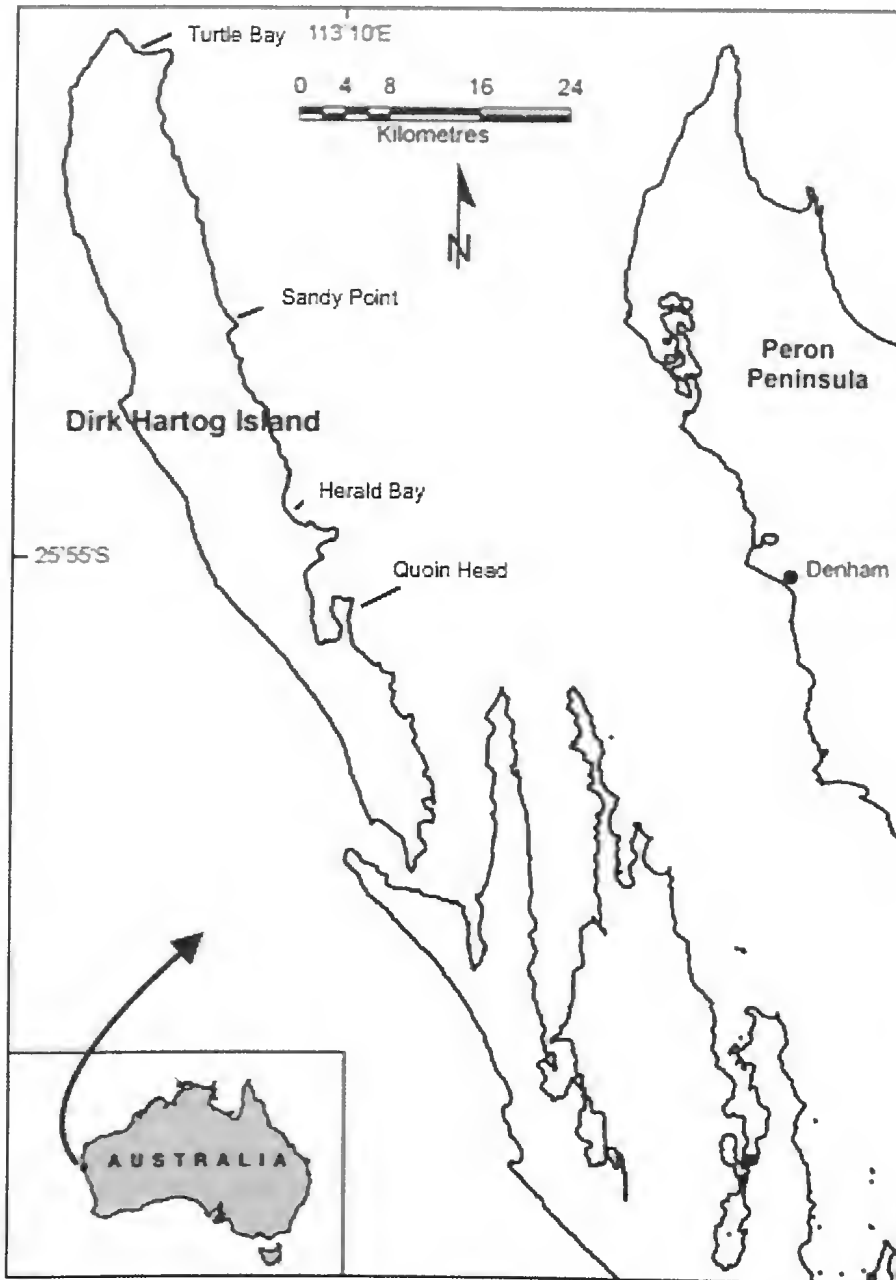


Figure 1. Dirk Hartog Island showing reference points of extent of study area (modified from Algar *et al.* 2011).

(terrestrial or inshore versus marine or offshore) (Peterson & Fry 1987; Hobson 1999; Rubenstein & Hobson 2004). Nitrogen stable isotopes are in turn used to determine trophic level and diet composition (Dahl *et al.* 2003; Morrison & Hobson 2004; Quillfeldt *et al.* 2008). Marine resources were expected to be part of the diet of feral cats on the island, since previous tracking data revealed distinct patrolling of beaches (Algar *et al.* 2011).

METHODS

Fieldwork was conducted from 27 March to 8 April 2013 on Dirk Hartog Island (25°50' S 113°0.5' E; Fig. 1). The island lies within the Shark Bay World Heritage Property and is the largest island in Western Australia, covering 620 km², spanning 79 km in length and a maximum of 11 km in width. The fieldwork was focused on the east coast

of the island, extending from Herald Bay in the south to Turtle Bay in the north (Fig. 1).

Feral cats were trapped over a period of 12 trapping nights and euthanized. The traps used in this study were covered padded leg-hold (soft catch) traps (Oneida Victor, size 3, Woodstream Corp., Lititz, Pa.; U.S.A) using cat faeces as the attractant. Sex and body weight were recorded in the field. All cat carcasses were frozen in the field before analysis in the laboratory. The cats were then dissected with muscle and liver tissue removed from the same location of each cat (shoulder and second lobe of the liver respectively).

Samples were thawed, sections of the gastrointestinal tract separated and then examined individually. The contents of the stomach were pooled with the contents of the small intestine. Food items were sorted macroscopically by eye. Identifiable material was sorted

into the five main food categories adapted from Risbey *et al.* (1999) of mammal, bird, reptile, invertebrate and plant material. Plant material was only classed as a food item if it contained fruits/berries, while other vegetation, such as sticks and leaves, were treated as incidental intake (Martin *et al.* 1996; Risbey *et al.* 1999). Mammal remains were identified by the presence of hairs, or identifiable body parts including legs and ears. Once all large identifiable samples had been removed from a section the remaining material was then washed twice through 1 mm mesh sieves (Coman & Brunner 1972; Risbey *et al.* 1999). Percentage occurrence was recorded as the number of stomachs containing a particular item as a percentage of the total fourteen stomachs examined. Proportion of occurrence was a visual estimate of the available space filled by an item.

Faeces was collected from the large intestine as no scats were collected from the field. Each faecal pellet was analysed whole as a prey item can occur in multiple sections of the same scat (Nogales *et al.* 1988). The identification of prey and the sieving process followed the same procedure as that of stomach contents.

Reference samples of prey species were collected opportunistically from the field. These included crab, bait fish, sand goanna (*Varanus gouldii*) and cormorant feathers (*Phalacrocorax* species). Samples were freeze-dried before being ground to a fine powder. Carbon and nitrogen isotope ratios were measured using a continuous flow system consisting of a Delta V Plus mass spectrometer connected with a Thermo Flush 1112 ConFlo IV (Thermo-finnigan/Germany). Between 0.7–0.8 mg of each animal tissue sample (muscle, liver, and feather) and 1.1–1.2 mg of faecal samples were combusted in a tin cup for the simultaneous determination of carbon and nitrogen isotope ratios. Multi-point normalization was used in order to reduce raw values to the international standard (Paul *et al.* 2007; Skrzypek *et al.* 2010). The statistical comparisons of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of individuals and areas were analysed using a one-way ANOVA.

Within-individual correlation of isotope ratios for different tissue types were analysed using a paired *t*-test.

RESULTS

Fourteen cats were trapped, comprising 11 males and three females. Twelve cats were trapped on the coastal tracks and two along the central track. Cats sampled had a mixed diet (Table 2), with animal items in 11 of 14 cats, and plant matter occurring in 6 of 14 cats. The major food categories found in stomachs were bird followed by reptile. Of the vegetative matter in stomachs no items were classed as food as none contained fruiting bodies. Invertebrates consisted mostly of an unidentified centipede species with some beetles. No stomach samples contained marine items.

The highest average proportions of stomach contents were again bird and reptile, both with a large variation (Fig. 2). The average proportion of mammalian remains in stomachs was 11.3%, with results as high as 50%. The highest proportion of reptile remains in stomachs was 90% and the highest proportion of bird remains in 14 stomachs was 55%.

Table 2. Percentage of feral cats from Dirk Hartog Island (of a total of 14) containing five major food categories and empty space, in stomachs and large intestines.

Category	Stomach (n = 14)	Large Intestine (n = 14)
	%	%
Mammal	35.7	42.8
Reptile	57.1	71.4
Bird	78.6	92.8
Invertebrate	28.6	64.3
Plant	42.8	0
Empty	42.8	14.3

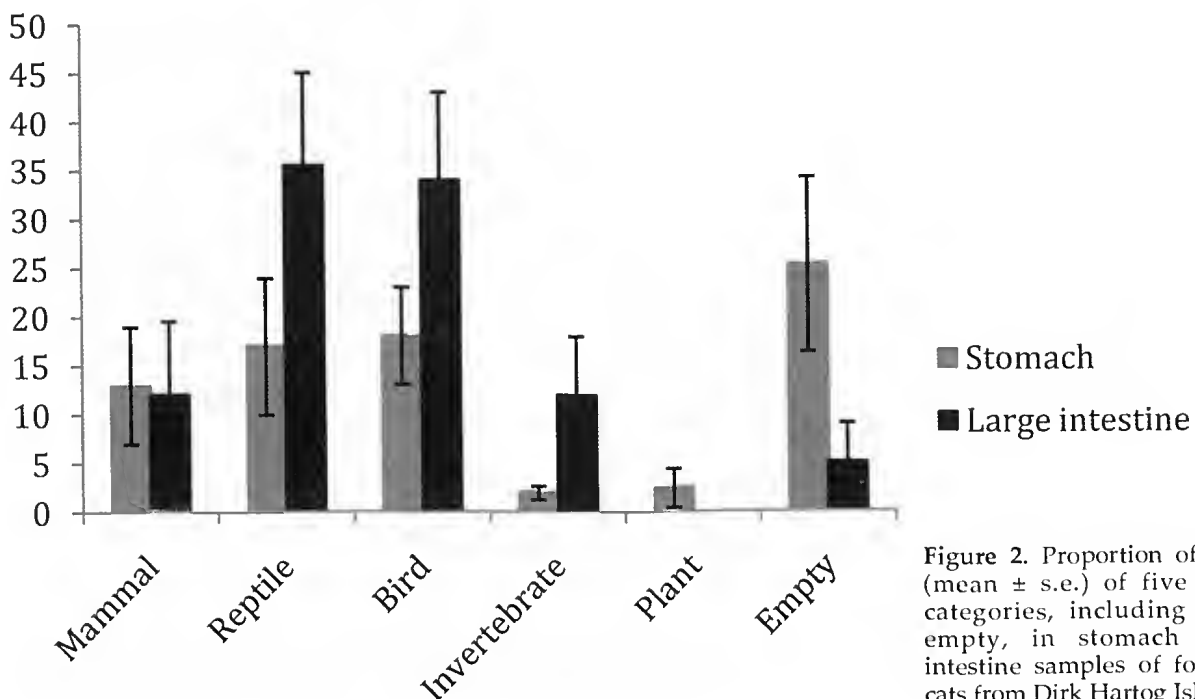


Figure 2. Proportion of occurrence (mean \pm s.e.) of five major diet categories, including proportion empty, in stomach and large intestine samples of fourteen feral cats from Dirk Hartog Island.

The large intestines all contained animal items with none containing plant matter (Table 2). Bird and reptile remains were also found most in the large intestine, occurring in 92.8% and 71.4% respectively, of all cats. There was a pronounced increase in the presence of invertebrate remains (62.4%) compared with the stomach contents. Mammal remains were identified in 6 of 14 cats. No large intestine samples contained marine items. Proportions of the five main food categories were calculated in all 14 large intestine samples (Fig. 2) and on average reptile and bird remains made up the largest proportion.

In the stomach and large intestine samples combined, there were several vertebrates identified to species level, including six birds and seven reptiles. Of the six birds, there were two terrestrial birds and four shorebirds (Table 3). Mammal remains were found in three of the fourteen cats and included cat hairs (presumably from self-grooming), one *Mus musculus* and two other small mammals that could not be identified to species level because of the small amount of material.

The carbon and nitrogen isotope ratios varied only slightly between terrestrial, coastal and marine reference samples (Fig. 3). The three habitat types overlapped considerably in $\delta^{15}\text{N}$, where the main difference was found in elevated levels in cormorant feathers collected from Sandy Point (Fig. 4). There was overlap in the carbon isotope ratio for reference samples from marine sources and seabird feathers, with a lower number for the terrestrial samples from *Varanus gouldii* (Fig. 3).

Cats were grouped based upon the trap line where they were caught (North, South and West). Consistent with the stomach and large intestine analysis, the carbon isotope ratios of muscle, liver and faeces showed a wide range (Fig. 4) with little overlap with the isotopic

Table 3. Vertebrate species identified from the digestive tracts of fourteen feral cats on Dirk Hartog Island.

Species name	Common name	Number of individual cats
Birds		
<i>Calamanthus campestris hartogi</i>	Rufous fieldwren	2
<i>Malurus lamberti</i>	Variegated fairy-wren	1
<i>Calidris canutus</i>	Red knot	1
<i>Calidris ruficollis</i>	Red-necked stint	1
<i>Haematopus longirostris</i>	Australian pied oystercatcher	1
<i>Himantopus himantopus</i>	Black-winged stilt	1
Reptiles		
<i>Ctenophorus sp</i>	Dragon lizard	5
<i>Pogona minor</i>	Western bearded dragon	1
<i>Ctenotus sp</i>	Skink	1
<i>Ctenotus fallens</i>	West-coast laterite Ctenotus	2
<i>Tiliqua rugosa</i>	Bobtail	1
<i>Varanus gouldii</i>	Gould's monitor	1
<i>Antaresia stimsoni</i>	Stimson's python	1
Mammals		
<i>Mus musculus</i>	House mouse	1

background data. The only sample type to differ between trapping lines was liver with carbon and nitrogen, $P = 0.025$ and $P = 0.002$ respectively (Table 4).

Within-individual correlation of the three sample types (faeces, liver and muscle) indicated some degree of individual consistency of diet, especially a strong correlation between liver and muscle samples. The evidence for a consistency of tissues with the last few

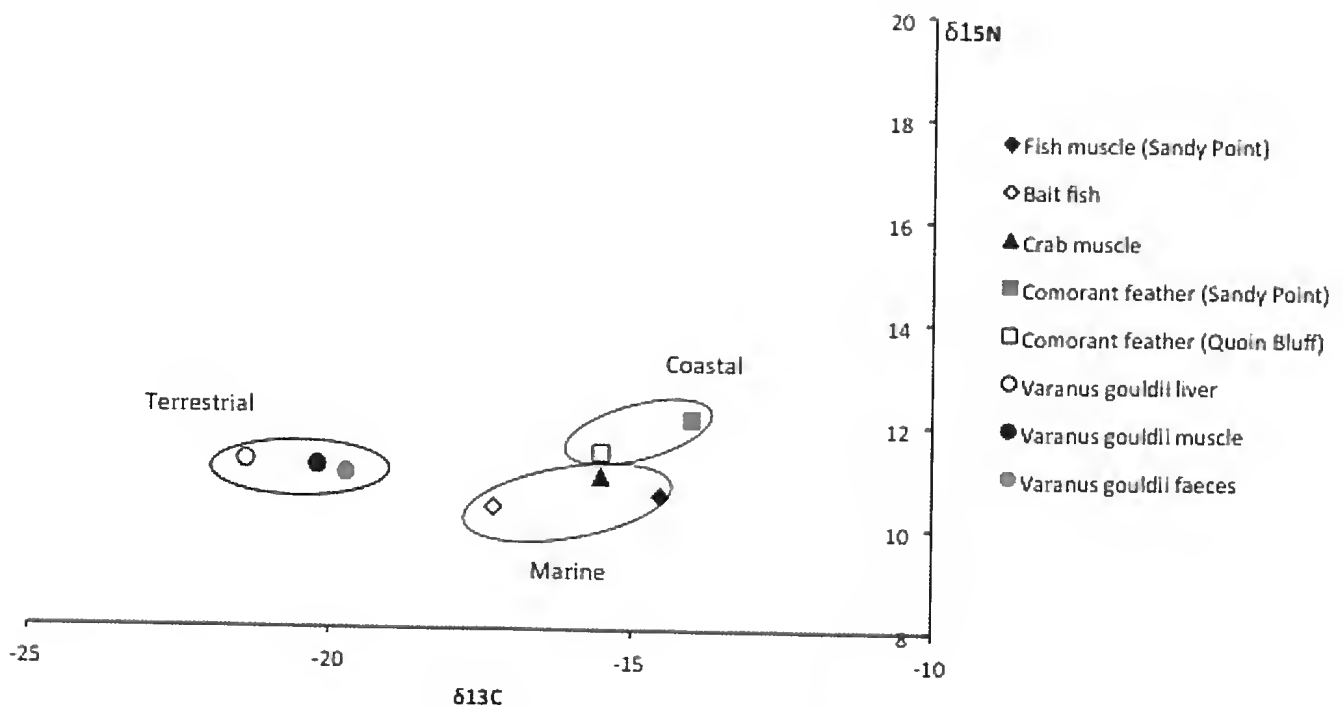


Figure 3. Carbon and nitrogen stable isotope ratios for reference material from different areas and habitat types on Dirk Hartog Island.

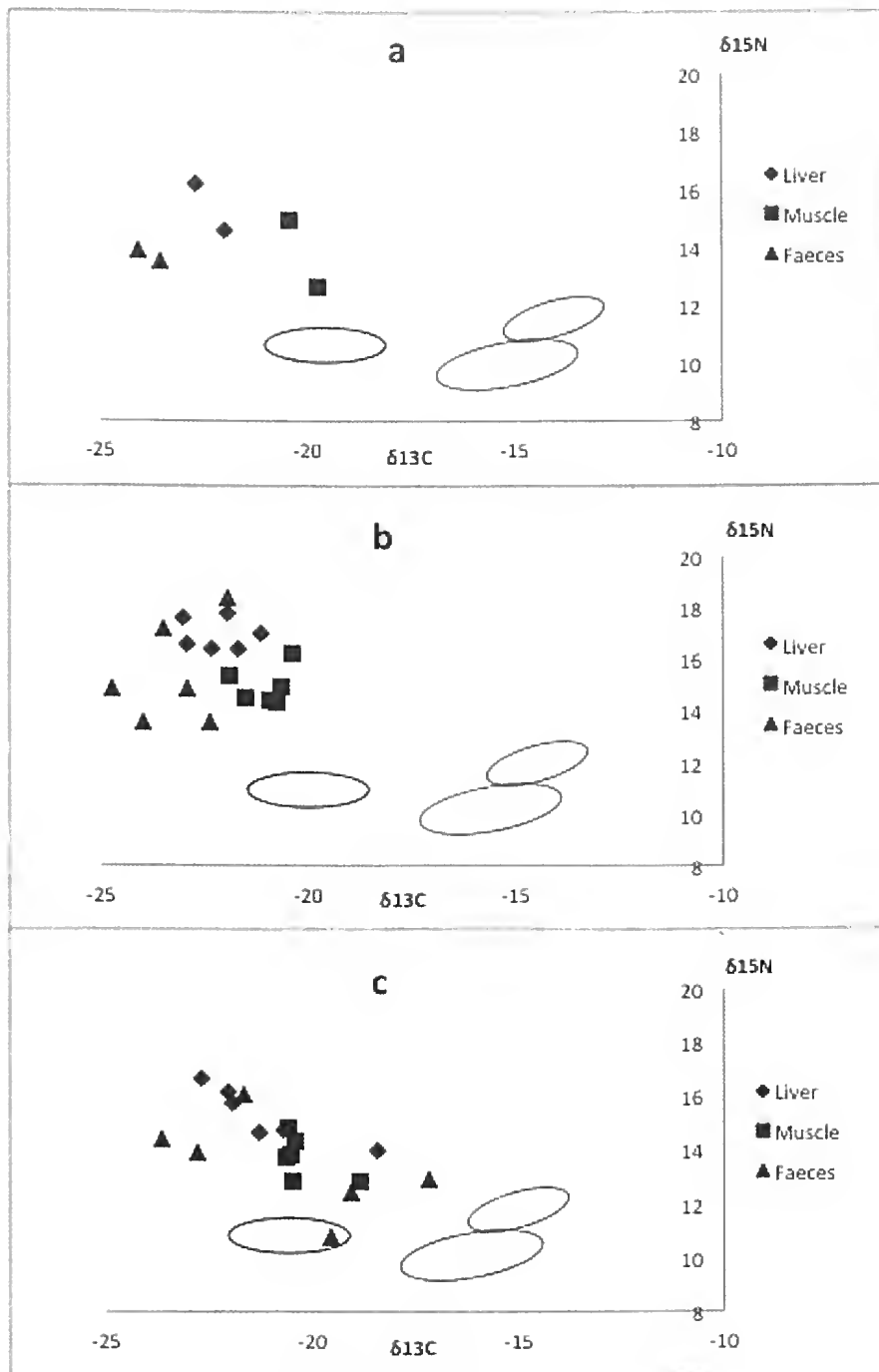


Figure 4. Carbon and nitrogen isotope stable isotope ratios for feral cats from a. Western, b. Southern and c. Northern trap lines on Dirk Hartog Island. Ovals represent values for reference samples shown in Figure 3.

Table 4. Stable isotope signatures of feral cats on Dirk Hartog Island (mean \pm s.e.) and results from multivariate ANOVA tests for differences between areas.

	Southern Line (n = 6)	Northern Line (n = 6)	Western Line (n = 2)	ANOVA results
Muscle				
$\delta^{13}\text{C}$	-21.01 ± 0.230	-20.24 ± 0.276	-20.09 ± 0.362	$P = 0.127$
$\delta^{15}\text{N}$	14.98 ± 0.297	13.76 ± 0.326	13.79 ± 1.154	$P = 0.107$
Liver				
$\delta^{13}\text{C}$	-22.17 ± 0.297	-21.17 ± 0.614	-22.36 ± 0.360	$P = 0.025$
$\delta^{15}\text{N}$	16.98 ± 0.250	15.34 ± 0.410	15.39 ± 0.840	$P = 0.002$
Faeces				
$\delta^{13}\text{C}$	-23.23 ± 0.424	-20.64 ± 1.010	-23.80 ± 0.273	$P = 0.095$
$\delta^{15}\text{N}$	15.41 ± 0.812	13.40 ± 0.745	13.72 ± 0.176	$P = 0.279$

Table 5. Within-individual correlation of isotope ratios for three sample types of feral cats on Dirk Hartog Island, P values from a paired t-test.

Sample type	Faeces	Liver
$\delta^{13}\text{C}$		
Muscle	0.003	<0.001
Faeces	–	0.159
Liver	–	–
$\delta^{15}\text{N}$		
Muscle	0.477	<0.001
Faeces	–	<0.001
Liver	–	–

meals (faeces) and short-term diet (liver) was mixed. The data for tissues and faeces (short-term diet) and muscle (long-term diet) were not correlated (Table 5).

DISCUSSION

The food items eaten by feral cats on Dirk Hartog Island were generally similar to those found for cats from mainland Western Australia and throughout other regions of Australia. One important difference was that whilst the major prey class throughout Australia is mammals, predominantly introduced rodents and rabbits (Coman & Brunner 1972; Catling 1988; Martin *et al.* 1996; Paltridge *et al.* 1997; Risbey *et al.* 1999), the major prey classes on Dirk Hartog Island were terrestrial birds and reptiles and thus it is these taxa that are most likely to benefit from the removal of cats. Since cats are opportunistic predators and scavengers (Coman & Brunner 1972; Nogales *et al.* 2004) whose diet is determined by the relative availability of prey species (Coman & Brunner 1972; Veitch 1985; Catling 1988), it is likely that the low percentage of occurrence of mammals in the diet of feral cats on Dirk Hartog Island can be explained by a low abundance of native mammals, and especially by the absence of introduced rabbits and rats.

The vertebrate species identified in the digestive tracts of cats included at least six bird species, including two terrestrial birds and four shorebirds, seven reptile species, and at least one mammal (*Mus musculus*). One of the bird species, the rufous fieldwren (*Calamanthus campestris hartogi*) is classified as vulnerable under the Environment Protection and Biodiversity Conservation Act 1999. Since the fieldwork was conducted in autumn, outside the spring breeding season of the majority of birds inhabiting the island (Johnstone *et al.* 2000), it is likely that the sampling underestimated the number of bird species that may be preyed upon by cats.

The analysis of remains in the digestive tract found no evidence of marine species being consumed. This was somewhat surprising, as Algar *et al.* (2011) reported that many cats on Dirk Hartog Island were found in coastal or near-coastal areas, so it was expected that cats may have predated or scavenged on fish or other marine detritus. Turtle hatchlings were expected to form part of the diet seasonally (Hilmer *et al.* 2010), but were not detected in the digestive tracts, despite being present on the island during the study. There was evidence,

however, of at least four species of shorebirds being either preyed on or scavenged – the red knot (*Calidris canutus*), red-necked stint (*Calidris ruficollis*), Australian pied oyster catcher (*Haematopus longirostris*) and the black-winged stilt (*Himantopus himantopus*).

Although no marine items were found in the analysis of stomach or intestinal contents, the stable isotope analysis of cats from the northern trap line showed some evidence of a potentially marine-derived diet. The carbon isotope ratio of faeces, muscle and liver showed a result similar to that of marine reference samples as well as that of previous studies ($\delta^{13}\text{C}$ of -20 to -16; Quillfeldt *et al.* 2008). This may reflect cats scavenging food along shorelines, or may partly reflect cats preying on species such as the shorebirds, which would presumably have an isotopic signature similar to marine fauna (Hobson 1987). The amount of isotopic reference samples was limited in this study because reference material was collected opportunistically in the field. Ideally, a more comprehensive number of reference samples from all potential prey species would have been collected to allow for more accurate identification of prey species, but time and budget constraints prevented this.

The locations available for trapping on Dirk Hartog Island were also limited, to along existing tracks and beach fronts, due to the density of vegetation. This limitation resulted in the inland portion of the island being difficult to trap extensively, whereas the coastal areas were relatively accessible with many tracks and beaches. The number of feral cats caught during this study was also limited by the amount of time available for trapping, and possibly because a previous trapping and pilot baiting program (Algar *et al.* 2011) had reduced the population size.

Feral cats showed a high consistency between liver and muscle isotope ratios, and thus probably had a consistent diet for a time of several weeks. This can be deduced due to the turnover rates of liver, one week, and muscle, four weeks (Tieszen *et al.* 1983). The mixed consistency between liver and faecal isotope ratios possibly reflects the opportunistic nature of feeding behaviour that is well documented in feral cats. It was expected that there would be very little consistency between muscle and faecal isotope ratios as they represent the most distinct sample types in terms of dietary time scale.

The findings of this study suggest that cats may be food-deprived during late autumn, as shown by the large percentage occurrence of empty stomachs at this time. This could be beneficial for management of cats, as late autumn is the period for toxic baiting as part of the eradication process. As reptiles are one of the major prey classes of cats on Dirk Hartog Island, the timing of baiting must also consider their abundance.

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REFERENCES

- ALBERTS A 2000. *West Indian iguanas: status survey and conservation action plan*. World Conservation Union, Cambridge.
- ALGAR D, JOHNSTON M & HILMER S S 2011. A pilot study for the proposed eradication of feral cats on Dirk Hartog Island, Western Australia. In: Veitch C R, Clout M N & Towns D R (eds) *Island invasives: eradication and management*, pp. 10–16. IUCN, Gland, Switzerland.
- BAYNES A 1990. The mammals of Shark Bay, Western Australia. In: Berry P F, Bradshaw S D & Wilson B R (eds) *Research in Shark Bay – Report of the France-Australe Bicentenary Expedition Committee*, pp. 313–325. Western Australian Museum, Perth.
- BEROVIDES V & COMAS A 1991. The critical condition of hutias in Cuba. *Oryx* 25, 206–208.
- BURBIDGE A 2001. Our largest island. *Landscape* 17, 16–22.
- BURBIDGE A & MANLY B F J 2002. Mammal extinctions on Australian islands: causes and conservation implications. *Journal of Biogeography* 29, 465–473.
- CATLING P C 1988. Similarities and contrasts in the diet of foxes, *Vulpes vulpes*, and cats, *Felis catus*, relative to fluctuating prey populations and drought. *Australian Wildlife Research* 15, 307–317.
- COMAN B J & BRUNNER H 1972. Food habits of the feral house cat in Victoria. *Journal of Wildlife Management* 36, 848–853.
- DAHL T M, FALK-PETERSEN S, GABRIELSEN G W, SARGENT J R, HOP H & MILLAR R M 2003. Lipids and stable isotopes in common eider, blacklegged kittiwake and northern fulmar: a trophic study from an Arctic fjord. *Marine Ecology Progress Series* 256, 257–269.
- FITZGERALD B M 1988. Diet of domestic cats and their impact on prey populations. In: Turner D C & Bateson P (eds) *The domestic cat: the biology of its behaviour*, pp. 123–147. Cambridge University Press, Cambridge.
- FULLER E 2000. *Extinct birds*. Oxford University Press, Oxford.
- GANNES L Z, MARTINEZ DEL RIO C & KOCH P 1998. Natural abundance variations in stable isotopes and their potential uses in animal physiological ecology. *Rapid Communication in Mass Spectrometry* 119, 725–737.
- GIBBONS J 1984. Iguanas of the South Pacific. *Oryx* 18, 82–91.
- HILMER S S, ALGAR D & JOHNSTON M 2010. Opportunistic observation of predation of loggerhead turtle hatchlings by feral cats on Dirk Hartog Island, Western Australia. *Journal of the Royal Society of Western Australia* 93, 141–146.
- HOBSON K A 1987. Use of stable isotope analysis to estimate marine and terrestrial protein content in gull diets. *Canadian Journal of Zoology* 65, 1210–1212.
- HOBSON K A 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120, 314–326.
- IVERSON J B 1978. The impact of feral cats and dogs on populations of the West Indian rock iguana, *Cyclura carinata*. *Biological Conservation* 14, 63–73.
- JOHNSTONE R E, BURBIDGE A H & STONE P 2000. Birds of the southern Carnarvon Basin, Western Australia: distribution, status and historical changes. *Records of the Western Australian Museum Supplement No. 61*, 371–448.
- KELLY J F 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology* 78, 1–27.
- MARTIN G R, TWIGG L E & ROBINSON D J 1996. Comparison of the diet of feral cats from rural and pastoral Western Australia. *Wildlife Research* 23, 475–484.
- MITCHELL N, HAEFFNER R, VEER V, FULFORO-GARDNER M, CLERVEAUX W, VEITCH C R & MITCHELL G 2002. Cat eradication and the restoration of endangered iguanas (*Cyclura carinata*) on Long Cay, Caicos Bank, Turks and Caicos Islands, British West Indies. In: Veitch C R & Clout M N (eds) *Turning the tide: the eradication of invasive species*, pp. 206–212. World Conservation Union, Gland, Switzerland.
- MCKENZIE N L, HALL N & MUIR W P 2000. Non-volant mammals of the southern Carnarvon Basin, Western Australia. *Records of the Western Australian Museum Supplement* 61, 479–510.
- MORRISON R I G & HOBSON K A 2004. Use of body stores in shorebirds after arrival on high-arctic breeding grounds. *Auk* 121, 333–344.
- NOGALES M, MARTIN A, DELGADO G & EMMERSON K 1988. Food spectrum of the feral cat (*Felis catus* L., 1758) in the juniper woodland on El Hierro (Canary Islands). *Bonner Zoology Beitrage* 39, 1–6.
- NOGALES M, MARTIN A, TERSHY B R, DONLAN C, VEITCH D, PUERTA N, WOOD B & ALONSO J 2004. A review of feral cat eradication on islands. *Conservation Biology* 18, 310–319.
- NOWAK R M 1999. *Walkers mammals of the world*. Johns Hopkins University Press, Baltimore, Maryland.
- PALTRIDGE R, GIBSON D & EOWAROS G 1997. Diet of the feral cat (*Felis catus*) in Central Australia. *Wildlife Research* 24, 67–76.
- PAUL D, SKRZYPEK G & FORZIS I 2007. Normalization of measured stable isotope composition to isotope reference scale – a review. *Rapid Communications in Mass Spectrometry* 21, 3006–3014.
- PETERSON B J & FRY B 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18, 293–320.
- QUILLFELDT P, SCHENK I, MCGILL R A R, STRANGE I J, MASELLO J F, GLADBACH A, ROESCH V & FURNESS R W 2008. Introduced mammals coexist with seabirds at New Island, Falkland Islands: abundance, habitat preferences, and stable isotope analysis of diet. *Polar Biology* 32, 333–349.
- RISBEY D A, CALVER M C & SHORT J 1999. The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. 1. Exploring potential impact using diet analysis. *Wildlife Research* 26, 621–630.
- RUBENSTEIN D R & HOBSON K A 2004. From birds to butterflies: animal movement patterns and stable isotopes. *Trends in Ecological Evolution* 19, 256–263.
- SKRZYPEK G, SAOLER R & PAUL D 2010. Error propagation in normalization of stable isotope data: a Monte Carlo analysis. *Rapid Communications in Mass Spectrometry* 24, 2697–2705.
- STAPP P 2002. Stable isotopes reveal evidence of predation by ship rats on seabirds on the Shiant Islands, Scotland. *Journal of Applied Ecology* 39, 831–840.
- STAPP P, POLIS G A & SANCHEZ F P 1999. Stable isotopes reveal strong marine and El Nino effects on island food webs. *Nature* 401, 467–469.
- THIESSEN L L, BOUTON T W, TESOAILL K G & SLAEO N A 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia* 57, 32–37.
- VEITCH C R 1985. *Methods of eradicating feral cats from offshore islands in New Zealand*. International Council for Bird Conservation, Technical Publication 3, 125–141.

Mangrove-associated macroalgae and cyanobacteria in Shark Bay, Western Australia

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A taxonomic survey of the macroalgae and cyanobacteria associated with pneumatophores of the mangrove *Avicennia marina* in Shark Bay, Western Australia, recorded 51 species, comprising 7 Cyanobacteria (blue-green algae), 14 Chlorophyta (green algae), 3 Phaeophyceae (brown algae) and 27 Rhodophyta (red algae). Of these, 31 represent new records for Shark Bay, and the red algae *Gelidium minisculum*, *Bostrychiocolax australis* (a parasite on *Bostrychia radicans*), and *Dasya kristeninae* are newly recorded for Western Australia.

KEYWORDS: *Avicennia marina*, epiphyte, macroalgae, pneumatophores, range extensions, Shark Bay

INTRODUCTION

Shark Bay is a large marine embayment located in Western Australia's semi-arid mid-west. The bay is geologically recent and is separated from the Indian Ocean on its western side by a ridge of Pleistocene Tamala limestone that forms the Zuytdorp Cliffs, Steep Point and the western side of Dirk Hartog Island (Playford 1990). The underlying geology of the region is largely covered by Pleistocene and Holocene sediments that now dominate marine and terrestrial habitats across much of the bay. Shark Bay's typically shallow marine environment comprises western and eastern gulfs separated by the Peron Peninsula. The complex bathymetry formed by channels, banks and sills constrains circulation and contributes to the persistence of hypersaline conditions in the south-eastern reaches at L'haridon Bight and Hamelin Pool. These features are markedly different to the adjacent high-energy oceanic environment and the bay is recognized as being biogeographically unique in the region (DEH 2006).

The distinctive physical and biological features of Shark Bay have led to the region's inclusion on the World Heritage List (whc.unesco.org), and the WA Government manages the bay's world heritage values under an agreement with the Australian Government. Conservation values are also managed by inclusion of marine and terrestrial areas in WA's reserve system, including the Shark Bay Marine Park and Hamelin Pool Marine Nature Reserve which were created in 1990 and comprise ca. 750 000 ha (CALM 1996).

Seagrasses and soft sediments form the major marine benthic habitats in Shark Bay, along with smaller areas of sponge-dominated habitat, corals and mangrove. The limited presence of marine rocky substrata means that macroalgal communities are not a prominent benthic feature as they are along the adjacent coast. Macroalgae occur on limited areas of rocky reef and pavement at

mostly western locations in the bay, as epiphytes on seagrasses and mangroves, and where they have colonized artificial structures like jetties and piers. A review by Huisman *et al.* (1990) documented 153 species of marine algae from Shark Bay.

A sole mangrove species, the Western white mangrove *Avicennia marina* var. *marina* (Fig. 2a, b), inhabits Shark Bay, which is the southern-most location where it forms extensive growth in WA. A general account of *A. marina* in Shark Bay is given in Kendrick *et al.* (2009). About 1,500 ha of *A. marina* exists in dense but often isolated stands around the bay, most of which are less than 10 ha in size and few of which exceed 100 ha (DPaW data). Notably, these trees and their pneumatophores can form a significant source of intertidal hard substratum across large parts of this sand-dominated bay where rocky substrata are scarce.

The suite of algal epiphytes associated with mangrove pneumatophores typically includes species associations that are rarely found in other habitats. Genera commonly found on (but not exclusive to) mangroves include the red algae *Bostrychia* and *Caloglossa*, plus a selection of generalist epiphytes such as *Spyridia filamentosa*, *Anotrichium tenue* and *Sphacelaria rigidula*. As part of a study of *A. marina* in the Shark Bay Marine Park, we undertook a taxonomic survey of the associated epiphytes, primarily to document their presence but also to examine whether species or species associations were unique to particular sites within the bay.

MATERIALS AND METHODS

Field work was undertaken during June 2009 and 13 sites of relatively dense mangrove growth were selected at spatially dispersed locations across Shark Bay (Fig. 1). At each site the occurrence of epiphytes was noted and where possible photographed *in-situ*. Representative samples of epiphyte-bearing pneumatophores were collected and preserved in a 5% Formalin/seawater solution. In the laboratory, larger epiphytes were pressed

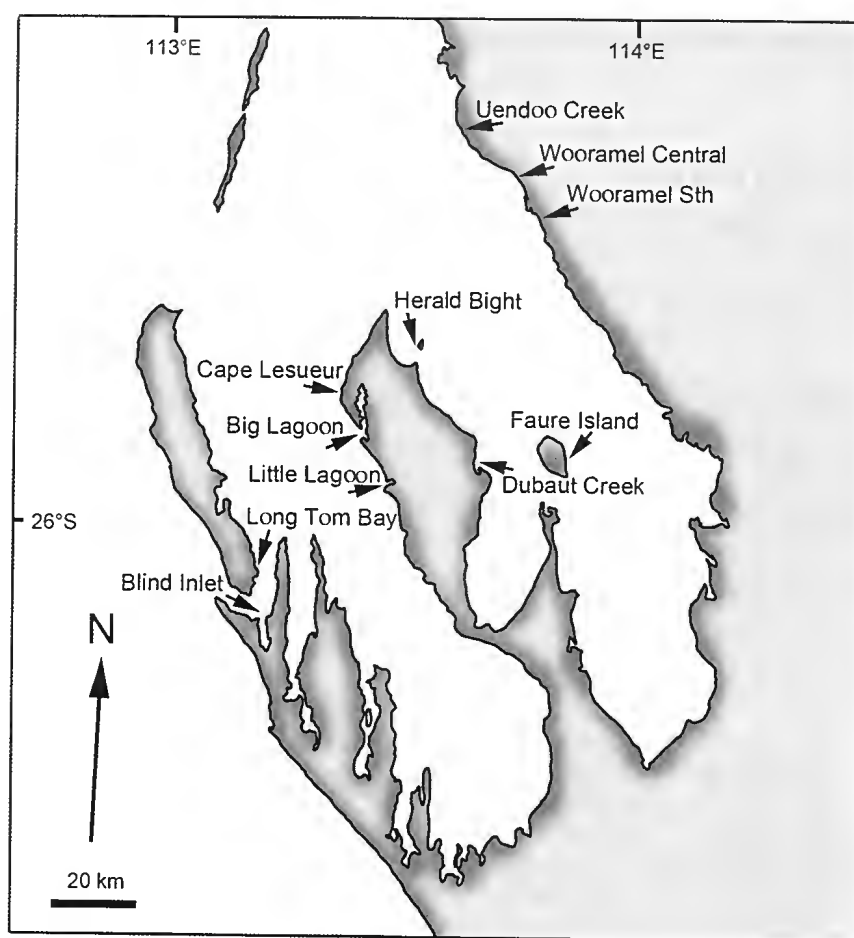


Figure 1. Map of Shark Bay showing collection localities.

onto herbarium sheets, while smaller specimens were mounted whole on microscope slides. Where necessary for microscopic examination, specimens were hand-sectioned, stained in aniline blue, and mounted in a solution of 50% Karo syrup and freshwater. Microscope preparations were examined and photographed using either a Nikon SMZ800 stereo microscope or a Nikon Eclipse 80i compound microscope, in both cases with a Nikon DS Fi1 digital camera. All herbarium sheets and microscopic preparations have been lodged in the Western Australian Herbarium (PERTH). The distribution of species at the various sites (Table 1) is based on presence as observed during the survey, and on subsequent laboratory examination of smaller species.

Only species intimately associated with pneumatophores were recorded. These were growing either directly on the pneumatophores (primary epiphytes) or attached to these primary epiphytes (secondary epiphytes). Some taxa (such as *Chaetomorpha*) were mostly unattached and entangled amongst the pneumatophores.

Taxa were identified based on morphology and agree with previously published accounts of the relevant species. In several cases, particularly in the Cyanobacteria, the identifications are tentative and confirmation by molecular analyses is highly desirable.

Arrangement of the taxonomic account

Taxonomic results are grouped into Cyanobacteria (= blue-green algae), Phaeophyceae (= brown algae),

Chlorophyta (= green algae), and Rhodophyta (= red algae), with constituent species listed alphabetically. This arrangement generally follows that of Huisman *et al.* (2011). For each species, the name, authority, and date and page of publication are given (the place of publication listed in the references), with author names abbreviated according to Brummitt & Powell (1992). Species newly recorded for Shark Bay are marked with an asterisk (*). The PERTH voucher is cited, followed by a comments section. Descriptions of specimens are based on the Shark Bay material. Unless otherwise indicated by 'epiphytic on...', the algae were growing directly on the *Avicennia marina* pneumatophores.

PREVIOUS RECORDS

The diversity of mangrove-associated algae in Shark Bay has not been studied intensively, but several species from the bay have been recorded in monographs and other studies. King & Puttock (1994a, b) surveyed Australian mangrove-associated red algae and recorded *Bostrychia moritziana*, *B. radicans*, *Caloglossa leprieurii*, *Polysiphonia scopulorum*, *Caulacanthus indicus* and *Gelidium* spp. for the region extending from Cape Cuvier to Cape Naturaliste, but no records specifically attributed to Shark Bay were included. Two species of *Bostrychia* often found on mangrove pneumatophores, *B. radicans* and *B. moritziana*, were recorded from Steep Point, Shark Bay, by King & Puttock (1989), although specific habitat details were not given. The collector of these specimens was Fred Wells, at the time with the Western Australian Museum, who

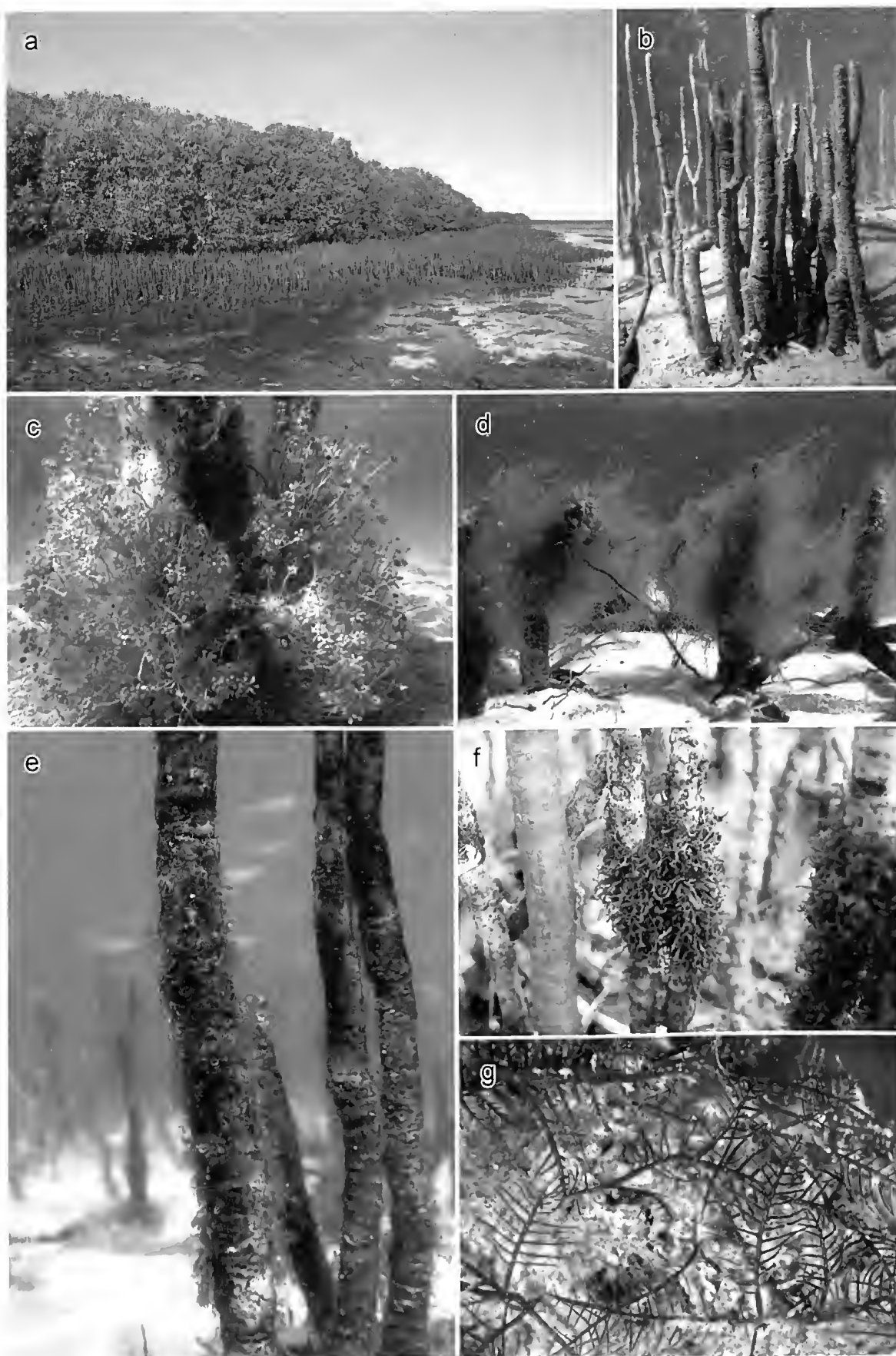


Figure 2. Habitat views and *in-situ* specimens. a. The mangrove *Avicennia marina* growing on the coast near Uendoo Creek. A dense stand of pneumatophores can be seen in the foreground. b. Pneumatophores from the Herald Bight stand, with no epiphyte growth. c. *Acetabularia peniculus* on pneumatophores at Wooramel Central. d. *Ulva flexuosa* on pneumatophores at the seaward edge of Big Lagoon. e. The leafy green *Gayralia oxysperma* on pneumatophores at the same site. f. A dense band of *Caloglossa leprieurii* on pneumatophores at Uendoo Creek. g. Close view of *Bostrychia flagellifera*.

Table 1. Algae and cyanobacteria epiphytic on *Avicennia marina*, Shark Bay, June 2009.

	Uendoo Creek	Wooramel Central	Wooramel South	Little Lagoon	Big Lagoon	Cape Lesueur	Dubaut Creek	Herald Bight	Faure North East	Faure South	Blind Inlet West	Blind Inlet East	Long Tom Bay
<i>Acetabularia peniculus</i>		X	X										
<i>Aglaothamnion cordatum</i>		X		X									
<i>Anotrichium tenne</i>	X			X									
<i>Blastophysa rhizopus</i>			X										
<i>Boodleopsis siphonacea</i>		X								X			X
<i>Bostrychia flagellifera</i>									X	X	X	X	X
<i>Bostrychia moritziana</i>													X
<i>Bostrychia radicans</i>	X												
<i>Bostrychia tenella</i>	X		X	X						X			X
<i>Bostrychiocolax australis</i>	X												
<i>Caloglossa lepreurii</i>	X		X	X						X			X
<i>Caloglossa monosticha</i>	X						X						
<i>Calothrix aeruginea</i>				X		X							
<i>Catenella uipae</i>	X		X							X			
<i>Centroceras</i> sp.		X	X	X									
<i>Chaetomorpha lignistica</i>	X						X			X	X	X	X
<i>Chondria succulenta</i>			X	X									
<i>Cladophora patentiramea</i>				X									X
<i>Cladophora rupestris</i>				X									
<i>Cladophora vagabunda</i>		X	X	X									X
<i>Crouania</i> sp.			X										
<i>Coleofasciculus chthonoplastes</i>													X
<i>Dasya kristeniae</i>				X									
<i>Dichothrix niahensis</i>				X									
<i>Dictyota furcellata</i>		X											
<i>Erythrotrichia carnea</i>	X		X	X		X			X				
<i>Gayliella fimbriata</i>						X							
<i>Gayralia oxysperma</i>					X			X					
<i>Gelidium miniscolum</i>	X												
<i>Griffithsia heteromorpha</i>				X									
<i>Herposiphonia pacifica</i>	X			X		X							
<i>Herposiphonia tenella</i>		X		X									
<i>Laurencia</i> sp.				X									
<i>Lyngbya semiplena</i>					X	X							
<i>Myrionema</i> sp.	X			X									
<i>Myxohyella papuana</i>													X
<i>Polysiphonia infestans</i>		X	X	X		X			X	X			
<i>Polysiphonia scopulorum</i>	X			X									
<i>Polysiphonia teges</i>				X									
<i>Polysiphonia</i> sp.													
<i>Rhizoclonium riparium</i>	X	X			X	X	X			X			X
<i>Rivularia atra</i>								X					
<i>Scytonema crispum</i>		X				X	X	X	X	X	X	X	X
<i>Sphacelaria rigidula</i>	X			X		X							
<i>Spyridia filamentosa</i>		X	X	X									
<i>Stylonema alsidii</i>		X	X							X			
<i>Ulva flexuosa</i>					X						X		
<i>Ulva paradoxa</i>	X		X		X	X			X	X		X	
<i>Ulvella leptochaete</i>			X	X									
<i>Ulvella viridis</i>				X									
<i>Uronema marinum</i>									X	X			X

recalled (pers. comm., 1 Mar. 2012) that the specimens were indeed epiphytic on mangroves.

Kendrick *et al.* (1990: 48) noted that collections of epiphytes were made from the pneumatophores of the mangrove *Avicennia marina* in Shark Bay during 1986. They listed *Ulvaria oxysperma* [= *Gayralia oxysperma*], *Caloglossa lepriurii*, *Spyridia filamentosa*, *Bostrychia moritziana*, *B. radicans* and *B. tenella* ssp. *flagellifera* [= *Bostrychia flagellifera*], but no collection data were given. These records were provided by Robert King, who identified the specimens (Kendrick *et al.* 1990: 53). Huisman *et al.* (1990) collated new and published records of macroalgae from Shark Bay, but did not include the mangrove epiphytes mentioned by Kendrick *et al.* (1990).

Kamiya *et al.* (1997) described the new species *Caloglossa monosticha*, with the type locality of Derby, Western Australia. They also cited a specimen from 'Small' [presumably Little] Lagoon, Denham, collected in 1991. The specific habitat of this Shark Bay specimen was not stated, but the species was described as "often epiphytic on mangroves" (p. 104).

Finally, the molecular phylogenetic analysis of *Caloglossa* species by West *et al.* (2001: 187, Table 2) included *C. lepriurii* from Shark Bay (specific location not given) and *C. monosticha* from Monkey Mia, Shark Bay.

RESULTS

Key to the major groups of mangrove-associated macroalgae and cyanobacteria at Shark Bay

- 1 Thallus blue-green to dark green, forming unbranched or falsely branched filaments, in some with heterocytes; cells prokaryotic, lacking organelles, but occasionally granular in appearance **Cyanobacteria**
- 1: Thallus various shades of green, red or brown, with simple or complex construction, without heterocytes; cells eukaryotic, with organelles 2
 - 2 Thallus grass green **Chlorophyta**
 - 2: Thallus other colours 3
- 3 Thallus brown **Phaeophyceae**
- 3: Thallus red **Rhodophyta**

Cyanobacteria (blue-green algae)

Numerous unicellular and filamentous cyanobacteria were present on the *Avicennia* pneumatophores. The present treatment only deals with the conspicuous taxa.

Key to the mangrove-associated Cyanobacteria at Shark Bay

- 1 Trichomes aggregated in a common sheath or mucilage 2
- 1: Trichomes not aggregated 4
 - 2 Trichomes without heterocytes **2. Coleofasciculus chthonoplastes**
 - 2: Trichomes with heterocytes 3
- 3 Trichomes with false branching, 1- many in a branched sheath **3. Dichothrix utahensis**

- 3: Trichomes aggregated in a mucilage hummock **6. Rivularia atra**
- 4 Trichomes with heterocytes 5
- 4: Trichomes without heterocytes 6
- 5 Heterocytes intercalary, filaments with occasional false branching **7. Scytonema crispum**
- 5: Heterocytes basal, filaments unbranched **1. Calothrix aeruginea**
 - 6 Filaments branched, prostrate on larger algae .. **5. Myxohyella papuana**
 - 6: Filaments unbranched, generally entangled amongst other algae **4. Lyngbya semiplena**

1. Calothrix aeruginea Thur. ex Bornet & Flahault 1886: 358.*

Filaments 200–250 µm long, with a basal heterocyte. Sheath 10–12 µm diam. near base, tapering distally. Trichomes basally 7–10 µm diam., tapering gradually and evenly to the apices. Basal heterocyte dome-shaped, 7–10 µm diam (Fig. 3a).

Specimen: Herald Bight, seaward side, on basal region of *Gayralia oxysperma*, 8 June 2009, J.M.Huisman (PERTH 08578699).

The specimens closely match the description of this species in Whitton (2011).

2. Coleofasciculus chthonoplastes (Thur. ex Gomont) Siegesmund, J.R.Johans. & Friedl. 2008: 1575.*

Thallus blue-green, with several trichomes united in a common sheath. Trichomes unbranched, slightly constricted at the cross walls, 5–9 µm diam. Cells L:B ±1.5–2, not tapering, apical cell with rounded apex, noncalyptate (Fig. 3b).

Specimen: Long Tom Bay, South Passage, 11 June 2009, J.M.Huisman (PERTH 08578796).

The present specimen agrees morphologically with the description of this apparently widespread species by Siegesmund *et al.* (2008), but the identification should be confirmed by molecular analyses.

3. Dichothrix utahensis Tilden 1898 [1894–1909]: 288.*

Thallus forming upright tufts of one to numerous trichomes in a common branched sheath, the basal segment comprised of a single trichome, more distal segments with progressively increasing numbers of trichomes due to addition by false branching. Trichomes 2–7 µm diam., tapering to pointed apices that emerge from the sheath, cells L:B 0.2–10 (shortest near apices). Heterocytes basal on false branches, unipolar, dome-shaped, 5–12 µm diam., L:B 0.5–1, or intercalary and bipolar, to 20 µm long and 7 µm diam. (Figs 3c, d).

Specimens: Little Lagoon, 6 June 2009, J.M.Huisman (PERTH 08578702).

The specimens agree with the description of this species from the Caribbean by Littler & Littler (2000), which was also of thalli growing on mangrove prop roots. Amongst the species they recorded, *D. utahensis* was characterized by its narrow heterocytes (10–16 µm diam.) and the presence of intercalary as well as basal heterocytes, both

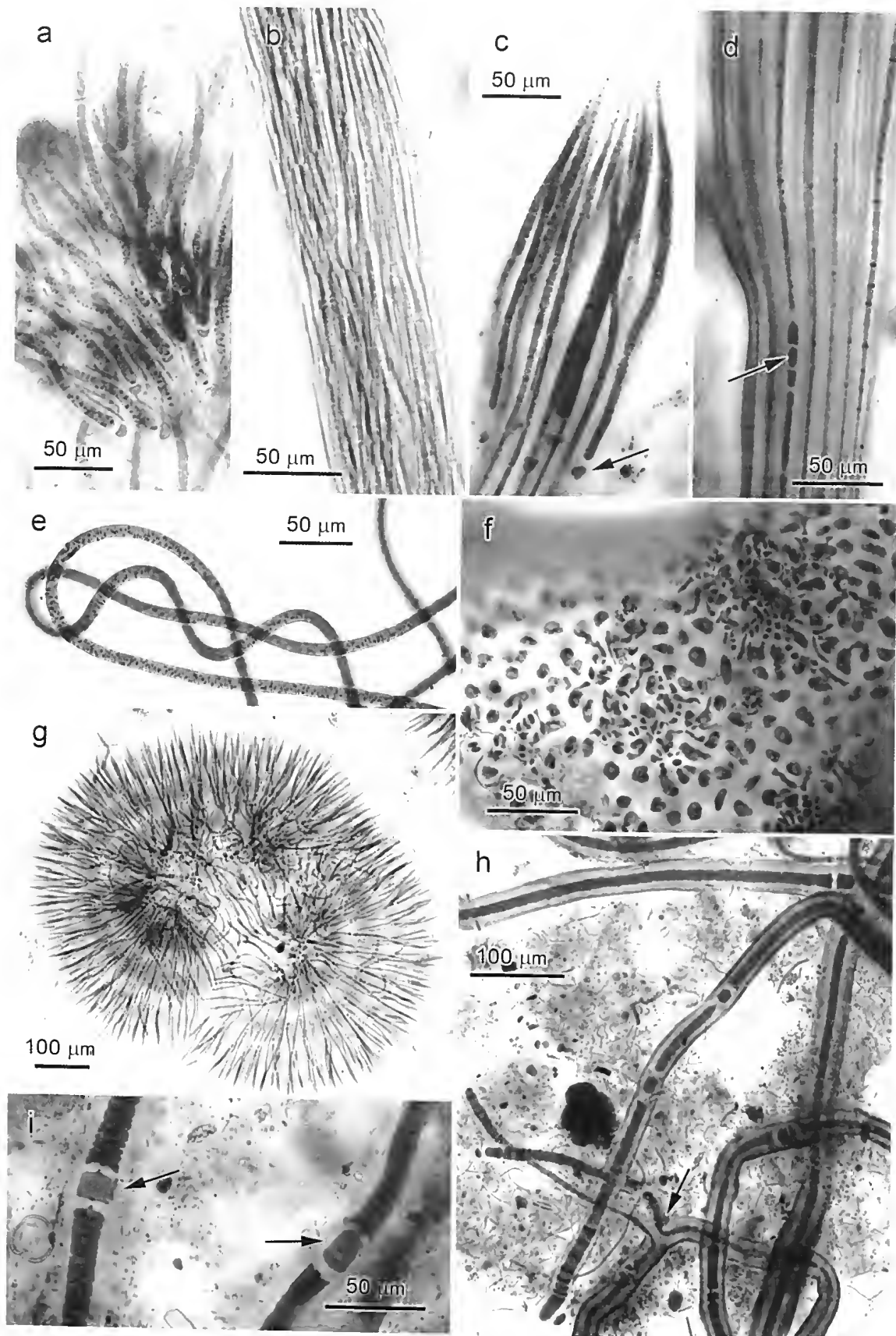


Figure 3. Cyanobacteria. a. *Calothrix aeruginea*, with clustered tapering trichomes and basal heterocysts. b. *Colcofasciculus chthonoplasies*, with numerous trichomes in a common sheath. c. *Dichothrix utahensis*, the wick-like upper region. d. *Dichothrix utahensis*, mid region with trichomes in a common sheath and intercalary heterocysts. e. *Lyngbya semiplena*. f. *Myxohyella papuana*, branched pseudofilaments growing on the surface of *Bostrychia tenella*. g. *Rivularia atra*, polar view of hemispherical colonies. h, i. *Scytonema crispum*. h. showing plate-like cells and conspicuous heterocysts (arrows). i. with false branching (arrow).

features of the Shark Bay material. The species was subsequently recorded from Wake Atoll in the central Pacific by Tsuda *et al.* (2010).

4. *Lyngbya semiplena* J.Agardh ex Gomont 1892: 138.*

Forming tangled mats. Filaments straight or occasionally coiled, unbranched, 7–12 µm diam., sheath inconspicuous. Cells discoid, L:B 0.2–0.3, with or without a terminal calyptra. Necridia common (Fig. 3e).

Specimen: Cape Lesueur, 7 June 2009, J.M.Huisman (PERTH 08578680).

This is a seemingly cosmopolitan species, found in coastal regions worldwide

5. *Myxohyella papuana* L.Hoffm. 1992: 318.*

Thallus blue-green, minute, 50–100 µm broad, prostrate and partly endophytic on *Bostrychia tenella*, with branched pseudofilaments. Central region of angular to rounded, mostly equidimensional cells, 3–5 µm diam. Peripheral cells elongate, L:B 2–7, often irregularly shaped and following the contours of the host cells (Fig. 3f).

Specimen: South Passage, epiphytic on *Bostrychia tenella*, 11 June 2009, J.M.Huisman (PERTH 08578575).

This small epiphyte was described from Papua New Guinea, based in part on a specimen 'endophytic in a red alga growing on the roots of mangrove trees in the intertidal zone'.

6. *Rivularia atra* Roth ex Bornet & Flahault 1886: 353.*

Colonies forming hemispherical hummocks, to 2 mm diam., formed by aggregated *Calothrix*-like filaments. Trichomes 150–400 µm long, with a dome-shaped basal heterocyte, ± 5 µm diam., then cells of similar diameter, L:B 0.5–1, gradually tapering to a hair-like apex (Fig. 3g).

Specimen: Little Lagoon, 6 June 2009, J.M.Huisman (PERTH 08578710).

Rivularia is a colonial organism formed of *Calothrix*-like trichomes embedded in mucilage.

7. *Scytonema crispum* Bornet ex Forti 1907: 498.*

Thallus tufted, to a few mm tall, often accumulating mud and other debris. Filaments mostly tortuous, occasionally straight, rarely with false branching, 25–35 (–50) µm diam., of fairly uniform width. Trichome blue-green, often filling sheath, especially near apices, to 15–25 µm diam., cells L:B 0.1–0.3, often considerably more slender in lower portions, to 3–7 µm diam., L:B up to 2, and occupying ± 15% of the sheath. Apices rounded or tapering, often with a cap-like apical cell. Heterocytes conspicuous, intercalary, with diameter similar to that of adjacent cells, L:B 0.5–2 (Figs 3h, i).

Specimen: Dubaut Creek, 8 June 2009, J.M.Huisman (PERTH 08578451).

This species forms dense tufts on the pneumatophore surface. The false branching and presence of heterocytes places it in the genus *Scytonema*, but most species in the genus have considerably more slender filaments. The specimens agree well with the description in Whitton

(2011), although he recorded only freshwater habitat and the determination is therefore tentative. King & Wheeler (1985) recorded *Scytonema crispum* (C. Agardh) Bornet occurring as dense tufts on pneumatophores at Stuarts Point, N.S.W. An invalidly described species, *Scytonema hamelinii* Gebelein (in Logan, Hoffman, & Gebelein, 1974: 146, 194) was recorded from Hamelin Pool, Shark Bay. This species was presumably not a mangrove epiphyte and we are unaware of any extant material.

Chlorophyta

Key to the mangrove-associated Chlorophyta at Shark Bay

- 1 Thallus microscopic, single-celled, endophytic or epiphytic on larger algae 9. *Blastophlysa rhizopus*
- 1: Thallus microscopic or macroscopic, multicellular or siphonous 2
 - 2 Thallus microscopic 3
 - 2: Thallus macroscopic 5
 - 3 Thallus with prostrate branched filaments 4
 - 3: Thallus with upright unbranched filaments 21. *Uronema marimum*
 - 4 Filaments closely arranged; cells with hairlike extensions 19. *Ulvella leptochaete*
 - 4: Filaments with intervening spaces; cells lacking hairlike extensions 20. *Ulvella viridis*
5. Thallus radially symmetrical, with a central stalk and apical crown of gametangial rays 8. *Acetabularia peniculus*
- 5: Thallus not radially symmetrical, of other form 6
 - 6 Thallus with discrete cells 7
 - 6: Thallus branched but lacking discrete cells (siphonous construction) 10. *Boodlopsis siphonacea*
 - 7 Thallus filamentous, unbranched 8
 - 7: Thallus filamentous and branched, or of other structure 9
 - 8 Cells 70–100 µm in diameter 11. *Chaetomorpha ligustica*
 - 8: Cells 15–35 µm in diameter 16. *Rhizoclonium riparium*
 - 9 Thallus filamentous, branched, never multiseriate, 10
 - 9: Thallus membranous or tubular, or partly multiseriate with uniseriate apices 12
 - 10 Thallus forming decumbent clumps, with arching filaments 13. *Cladophora patentiramea*
 - 10: Thallus mostly upright 11
 - 11 Thallus with percurrent primary axis and often opposite lateral branches; not falcate near apices 14. *Cladophora rupestris*
 - 11: Thallus generally with only one lateral branch per cell; falcate near apices 12. *Cladophora vagabunda*
 - 12 Thallus membranous .. 15. *Gayralia oxysperma*
 - 12: Thallus not membranous 12
 - 13 Thallus lacking uniseriate branches .. 17. *Ulva flexuosa*
 - 13: Thallus with uniseriate branches near apices 18. *Ulva paradoxa*

8. *Acetabularia peniculus* (R.Brown ex Turner) Solms-Laubach 1895: 27.

Thallus generally with several upright axes in a cluster, pale green or whitish from calcification, to 10 cm tall, with several whorls of colourless branched hairs and an apical whorl of 10–18 green gametangial rays, these basally attached but not laterally joined. Gametangial rays clavate, 2–5 mm long and 0.5–3.0 mm broad, when fertile with numerous spherical gametangial cysts 240–270 µm diam. (Fig. 2c).

Specimen: Wooramel central, 5 June 2009, J.M.Huisman (PERTH 08578419).

Acetabularia peniculus is a common species that is often found growing in clusters on old bivalve shells on sandy substrata. This represents the first record of this species as a mangrove epiphyte. The species was included in the earliest records of marine algae from Shark Bay (Quoy & Gaimard 1824: 159, as *Polyphysa peniculus* from 'Baie des Chiens-Marins')

9. *Blastophysa rhizopus* Reinke 1889: 87.*

Individual, irregularly shaped, green cells, 35–50 µm broad, epiphytic on *Bostrychia tenella*.

Specimen: Wooramel, epiphytic on *Bostrychia tenella*, 5 June 2009, J.M.Huisman (PERTH 08578591).

This is a small epi/endophyte that is often associated with larger red algae.

10. *Boodleopsis siphonacea* A.Gepp & E.Gepp 1911: 64.*

Thallus tufted, dark green, to 5 mm tall, with prostrate and irregularly constricted siphons 50–75 µm diam., attached by tapering rhizoids 8–20 µm diam.; erect siphons terete, 17–25 µm diam. Branches 50–900 µm long, more elongate distally, evenly constricted at branch bases and often with slight constrictions elsewhere (Figs 4a, b).

Specimens: Faure I., Shark Bay, 10 June 2009, J.M.Huisman (PERTH 08578478); Blind Inlet, South Passage, Shark Bay, 11 June 2009, J.M.Huisman (PERTH 08578486).

This species is apparently known only from the type collection, but other species recorded from elsewhere might be synonymous. Species of *Boodleopsis* are distinguished by features such as habit, density of branching, and frequency of constrictions, which appear to overlap in many cases. Skelton & South (2002) described similar specimens from mangroves in Samoa, which they ascribed to *B. carolinensis* Trono, a species separated from *B. siphonacea* largely by its more densely branched habit (Trono 1971).

11. *Chaetomorpha ligustica* (Kütz.) Kütz. 1849: 376.*

Thallus grass green, generally entangled amongst other algae or cyanobacteria, composed of unbranched filaments. Cells 70–100 µm diam., L:B 1–3, intercalary divisions common and forming pairs of daughter cells. Parietal reticulate plastids with numerous pyrenoids. Rarely with attachment rhizoids (Fig. 3d) similar to those found in *Rhizoclonium* (Figs 4c, d).

Specimen: Long Tom Bay, 11 June 2009, J.M.Huisman (PERTH 08578400).

These specimens agree with Womersley's (1984) concept of *Chaetomorpha capillaris* (Kütz.) Borgesen, a species now regarded as a taxonomic synonym of *Chaetomorpha ligustica* (see Leliaert & Boedeker 2007: 142). Cribb (1965) treats this species as the basionym *Rhizoclonium capillare*, based on the presence of attachment rhizoids similar to those found in the present material, but Womersley (1984) doubted the specific identity of Cribb's material. Beanland & Woelkerling (1982: 94) recorded this species (as *C. capillaris*) on *Avicennia* pneumatophores in South Australia.

There is considerable uncertainty regarding specific identities of *Chaetomorpha* and *Rhizoclonium* species, and it is likely that several cryptic species are involved. Thus application of this name must be regarded as tentative in the absence of DNA sequence analyses.

12. *Cladophora patentiramea* (Mont.) Kütz. 1849: 416.*

Thallus forming a tuft, attached at several points, with arching, irregularly branched filaments. Rhizoids arising as projections from proximal end of bearing cell. Lateral branches initially in open connection with parent cell, later forming a cross-wall. Cells 70–160 µm diam., elongate, L:B up to 10.

Specimen: Long Tom Bay, South Passage, 11 June 2009, J.M.Huisman (PERTH 08578753).

13. *Cladophora rupestris* (L.) Kütz. 1843: 270.*

Thallus dark green, attached by digitate processes arising from the basal cell. Primary axis percurrent, with cells 70–100 µm diam., L:B 1–4, each generally with (1-) 2 (-3) opposite lateral branches, occasionally naked (Fig. 4e).

Specimen: Wooramel, epiphytic on *Bostrychia tenella*, 5 June 2009, J.M.Huisman (PERTH 08578745).

This distinctive species has dark green percurrent primary axes from which lateral branches arise in opposite pairs.

14. *Cladophora vagabunda* (L.) C.Hock 1963: 144.

Thallus upright, grass green, filamentous, generally branched every 1–2 cells but often with intercalated unbranched cells. Branching falcate near apices. Cells 70–80 µm diam. near base, tapering to 20–25 µm diam.

Specimen: Faure I., 10 June 2009, J.M.Huisman (PERTH 08578443).

The dimensions of these specimens fall within *Cladophora dalmatica* Kütz., a species now provisionally treated as a small form of *C. vagabunda* (e.g. Kraft 2007: 81), although molecular analyses will likely result in further revision. Previously recorded for Shark Bay by Huisman *et al.* (1990).

15. *Gayralia oxysperma* (Kütz.) Vinogradova ex Scagel *et al.* 1989: 72.

Thallus grass green, membranous, leafy, to 3 cm tall and equally as broad. Blade one cell thick, in surface view the cells often in packets. Lower cells with basally directed, elongate tails (Figs 2e, 4f).

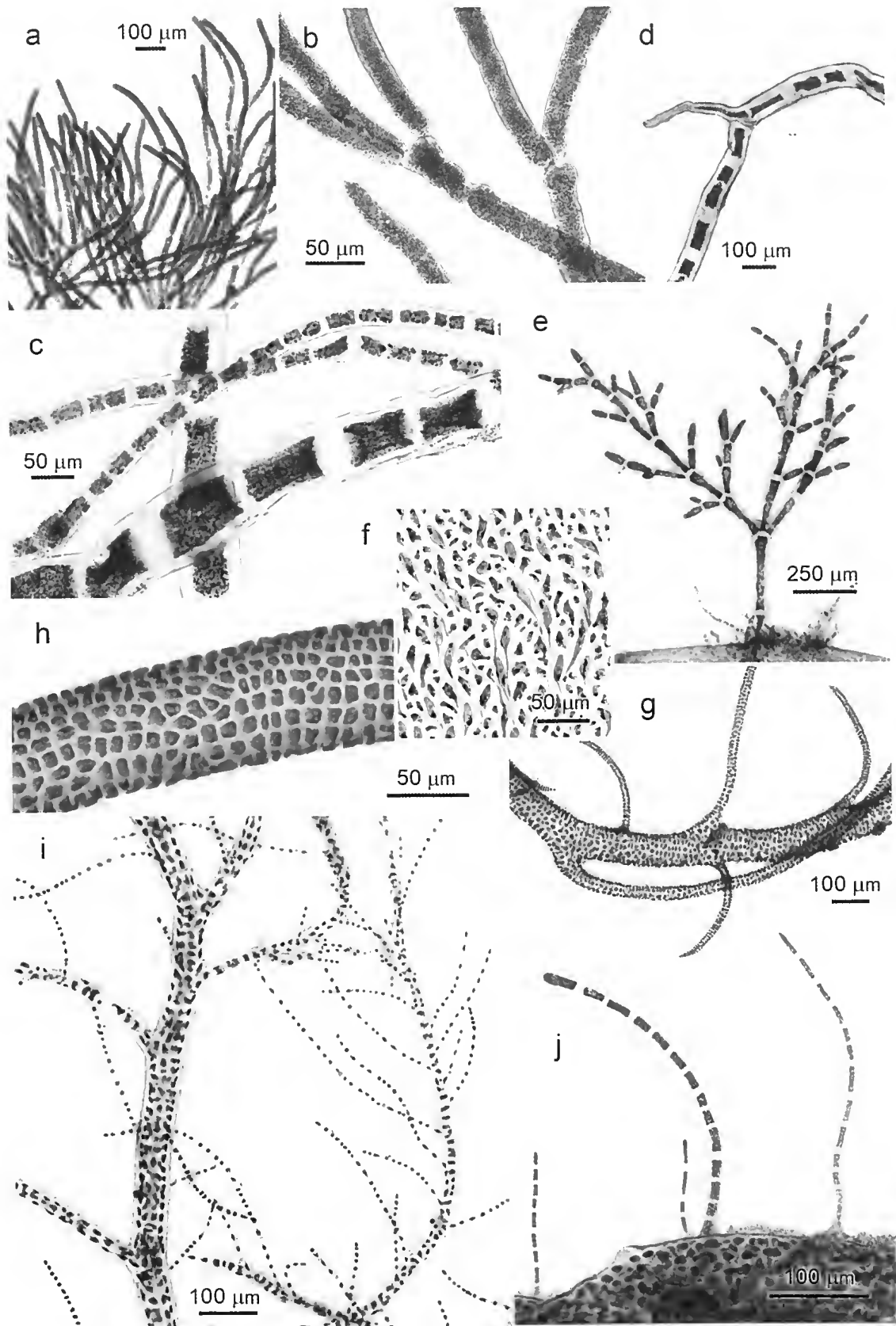


Figure 4. Chlorophyta (green algae). a, b. *Boodleopsis siphonacea*. a. view of upper thallus. b. detail of branching with slight constrictions. c. *Chaetomorpha ligustica* (broad, lower filaments) and *Rhizoclonium riparium* (narrow, upper filaments), often found growing together. d. *Chaetomorpha ligustica*, with attachment rhizoid. e. *Cladophora rupestris*, with branched filaments. f. Surface view of *Gayralia oxysperma*, at the transition to the basal region and showing cells with elongate tails. g, h. *Ulva flexuosa*. g. thallus habit. h. closer view of branch with cells in vague longitudinal rows. Several pyrenoids can be seen in each cell. i. *Ulva paradoxa*, thallus habit, showing numerous uniseriate branches characteristic of this species. j. *Uronema marinum*, simple filaments typical of this species.

Specimen: Big Lagoon, 7 June 2009, J.M.Huisman (PERTH 08578427).

The membranous green thallus of *Gayralia oxysperma* superficially resembles that of some leafy species of *Ulva* (see Kendrick *et al.* 2009: unnumbered fig. on p. 55), but it can be readily identified by its blades composed of only a single cell layer, whereas those of *Ulva* have two layers.

16. *Rhizoclonium riparium* (Roth) Harv. 1849: pl. CCXXXVIII.*

Slender unbranched filaments, growing indeterminately (vouchers to 5 mm long), sporadically attached to the pneumatophores by rhizoidal outgrowths from distal ends of cells, these causing the filament to kink. Filaments 15–35 µm diameter, cells L:B 1–3, intercalary divisions common and distinct pairs of daughter cells. Parietal plastids somewhat rod-shaped, with numerous pyrenoids (Fig. 4c).

Specimens: Uendoo Creek, 4 June 2006, J.M.Huisman (PERTH 08578672); Faure I., 10 June 2009, 10.17 a.m. J.M.Huisman (PERTH); Long Tom, South Passage, 11 June 2009, J.M.Huisman (PERTH).

17. *Ulva flexuosa* Wulfen 1803: 1.*

Thallus erect, to 7–8 cm tall, grass-green, attached by a rhizoidal base. Branching primarily from near the base; branches proximally narrow and broadening distally. Structure with cells mostly in longitudinal rows, occasionally also in transverse rows, the alignment of cells more regular near the base and becoming irregular above. Cells in surface view square to rectangular, 10–20 µm wide, each with a parietal chloroplast and 2–4 pyrenoids each 5–6 µm diam. (Figs 4g, h).

Specimen: Big Lagoon, Shark Bay, ocean side, on *Avicennia marina* pneumatophores, 7 June 2009, J.M.Huisman (PERTH 08578664).

Ulva flexuosa and *U. paradoxa* were previously included in the now subsumed genus *Enteromorpha*, a genus wherein the thallus was tubular in form rather than sheet-like as in typical *Ulva*. Thalli of *Ulva flexuosa* have tubular branches in which the cells are arranged in longitudinal and often transverse series. Adventitious uniseriate branches arise occasionally to profusely from the tubular branches. Each cell has 2–3 pyrenoids. *Ulva paradoxa* was once regarded as a form of *U. flexuosa*. It differs in the regular occurrence of uniseriate branches, these near apices often with opposite lateral branches.

18. *Ulva paradoxa* C.Agardh 1817: xxii.*

Thallus erect, to 5 cm tall, olive-green to grass-green, tufted, with a rhizoidal base. Primary axes 30–60 µm diam. Branching irregular, most axes with uniseriate lateral branches, these alternate or often opposite, 15–20 µm diam. Cells transversely and longitudinally aligned throughout, although often displaced, 10–35 µm diam. in surface view, each with 2–10 pyrenoids (Fig. 4i).

Specimen: Cape Lesueur, 7 June 2009, J.M.Huisman (PERTH 08578273).

19. *Ulvella leptochaete* (Huber) R.Nielsen, O'Kelly & B.Wysor in Nielsen *et al.* 2013: 51.*

Thallus microscopic, prostrate on *Acetabularia peniculus*, composed of branched filaments that generally coalesce to form a partly complete cover. Cells irregularly shaped, 20–35 µm diam., many with hairlike extensions.

Specimen: Wooramel, epiphytic on *Acetabularia peniculus*, 5 June 2009, J.M.Huisman (PERTH 08578737).

20. *Ulvella viridis* (Reinke) R.Nielsen, O'Kelly & B.Wysor in Nielsen *et al.* 2013: 53.*

Thallus microscopic, bright green, endophytic in walls of *Polysiphonia teges*, of irregularly branched prostrate filaments to 200 µm long. Filaments generally remaining free, rarely forming a loose pseudoparenchyma. Cells mostly subisodiametric, squarish to rectangular in outline, mostly 10–15 µm diam., but some cells in actively growing regions more slender (c. 5 µm diam.). Cells with a parietal chloroplast and 1 or 2 pyrenoids. Hairs not observed.

Specimen: Little Lagoon, on *Polysiphonia teges*, 6 June 2009, J.M.Huisman (PERTH 08578583).

21. *Urouema marinum* Womersley 1984: 131.*

Thallus grass green, with simple filaments to 400 µm tall, 7–17 µm diam., attached basally by a small digitate holdfast. Cells L:B 1.5–4, with one central nucleus and several pyrenoids (Fig. 4j).

Specimen: Faure I., epiphytic on *Bostrychia tenella*, 10 June 2009, J.M.Huisman (PERTH 08578761).

Phaeophyceae

The diversity of brown algae was very low, with only *Dictyota furcellata*, *Sphacelaria rigidula* and the small encrusting *Myrionema* sp. encountered.

Key to the mangrove-associated Phaeophyceae at Shark Bay

- 1 Thallus forming discoid crusts, less than 1 mm diam. **23. *Myrionema* sp.**
- 1: Thallus upright, not small crusts 2
 - 2 Thallus dichotomously branched, with flat axes **22. *Dictyota furcellata***
 - 2: Thallus tufted, wiry, irregularly branched, with terete axes **24. *Sphacelaria rigidula***

22. *Dictyota furcellata* (C.Agardh) J.Agardh 1848: 90.

Thallus to 8 cm tall, entangled, dichotomously divided every 5–10 mm. Axes flattened, to 1 mm broad below, tapering to 200 µm near apices. Apices pointed, with a prominent apical cell. Hair tufts common. Tetrasporangia scattered or in small groups on surface of thallus, spherical, 75–110 µm diam. (Fig. 5b).

Specimen: Wooramel central, 5 June 2006, J.M.Huisman (PERTH 08578370).

Shark Bay is the type locality of this narrow species of *Dictyota*.

23. *Myrionema* sp.*

Thallus epiphytic, discoid, to 350 µm diam., with a monostromatic basal layer of regularly or irregularly radiating filaments, these when mature bearing short upright filaments, phaeophycean hairs, or ascocysts. Basal filaments laterally coherent, except at margins where some are free, with cells quadrate or irregular in shape, 8–10 µm broad, L:B ±1. Phaeophycean hairs to 400 µm long, simple, with a basal meristem subtending hyaline cells 7–10 µm diam., L:B to 10.

Specimens: Little Lagoon, on *Polysiphonia tages*, 6 June 2009, J.M.Huisman (PERTH 08578648).

This is a small discoid epiphyte found on a variety of other algae. The specimens are not adequate for species determination.

24. *Sphacelaria rigidula* Kütz. 1843: 292.

Thallus to 10 mm tall, forming dense dark brown wiry tufts attached by rhizoidal filaments arising from lower axes. Erect axes mostly of similar height; apical cells 25–50 µm diam.; lower segments undergoing several longitudinal divisions, but maintaining a similar diameter throughout the plant, in lateral view showing 1–3 (–4) cells. Lateral branches common, arising at shallow angles and slightly narrowed at the base. Elongate hairs forming laterally near apices of erect axes, 20–25 µm diam., with a basal meristem. Propagules with a primary axis c. 250 µm long, bearing 2 elongate arms and a small dome-shaped cell at the apex (Fig. 5a).

Specimen: Little Lagoon, 6 June 2009, J.M.Huisman (PERTH 08578494).

Rhodophyta*Key to the mangrove-associated Rhodophyta at Shark Bay*

- 1 Thallus filamentous, structurally without pericentral cells, pseudoparenchyma or cortication of any form 2
- 1: Thallus structurally with pericentral cells, pseudoparenchyma or cortication 7
 - 2 Filaments without pit-connections between cells 3
 - 2: Filaments with pit-connections between cells 4
- 3 Thallus unbranched 39. *Erythrotrichia carnea*
- 3: Thallus branched 51. *Stylonema alsidii*
 - 4 Axial cells each with 3 whorl branches 37. *Crouania* sp.
 - 4: Axial cells with fewer than 3 branches 5
- 5 Thallus alternately branched with a single lateral branch per axial cell, without trichoblasts 25. *Aglaothamnion cordatum*
- 5: Thallus sparsely branched, with trichoblasts (colourless hairs) 6
 - 6 Cells mostly of similar form; trichoblasts numerous, very conspicuous 26. *Anotrichium tenue*
 - 6: Cells cylindrical in lower thallus, barrel-shaped to spherical in upper thallus; trichoblasts rudimentary 42. *Griffithsia heteromorpha*
- 7 Thallus cartilaginous, wiry, structurally with longitudinal medullary filaments and a pseudoparenchymatous cortex 8
- 7: Thallus not as above 9
 - 8 Thallus segmented, without rhizines 34. *Catenella nipae*
 - 8: Thallus not segmented, with rhizines (thick walled internal filaments) 41. *Gelidium minisculum*
- 9 Thallus leafy, with a midrib and lateral wings 10 (*Caloglossa*)
- 9: Thallus not leafy 11
 - 10 Attachment rhizoids forming a stipe; basal axial cell of lateral branches lacking an adaxial pericentral cell 32. *Caloglossa lepreurii*
 - 10: Attachment rhizoids not forming a stipe; basal axial cell of lateral branches with an adaxial pericentral cell 33. *Caloglossa monosticha*
- 11 Forming parasitic pustules on *Bostrychia* 31. *Bostrychiocolax australis*
- 11: Not parasitic 12
 - 12 Branches with pericentral cells (longitudinally oriented cells cut off from the primary axial cells) 13
 - 12: Branches without pericentral cells 25
- 13 Pericentral cells divided transversely ... 14 (*Bostrychia*)
- 13: Pericentral cells not divided transversely 17
 - 14 Thallus with main axes corticate 15
 - 14: Thallus ecorticate throughout 16
- 15 Lateral branches arising from every axial cell on the indeterminate axes 30. *Bostrychia tenella*
- 15: Lateral branches arising from every 2–4(–5) axial cells on the indeterminate axes .. 27. *Bostrychia flagellifera*
 - 16 All branches polysiphonous 29. *Bostrychia radicans*
 - 16: Main branches polysiphonous; ultimate vegetative branches monosiphonous 28. *Bostrychia moritziana*
- 17 Thallus with distinct prostrate axes from which arise upright branches in a regular pattern of determinate and indeterminate branches 18 (*Herposiphonia*)
- 17: Thallus erect, or if prostrate without a regular pattern of branches 19
 - 18 Lateral branches in the repeating pattern: 3 determinate/1 determinate 44. *Herposiphonia tenella*
 - 18: Lateral branches in the repeating pattern: 1 determinate/1 determinate/1–2 naked segments 43. *Herposiphonia pacifica*
- 19 Thallus with pigmented monosiphonous filaments 38. *Dasya kristeniae*
- 19: Thallus with unpigmented monosiphonous filaments (= trichoblasts) 20
 - 20 Thallus with secondary cortication obscuring the pericentral cells 21
 - 20: Thallus without secondary cortication, with visible pericentral cells 22 (*Polysiphonia*)

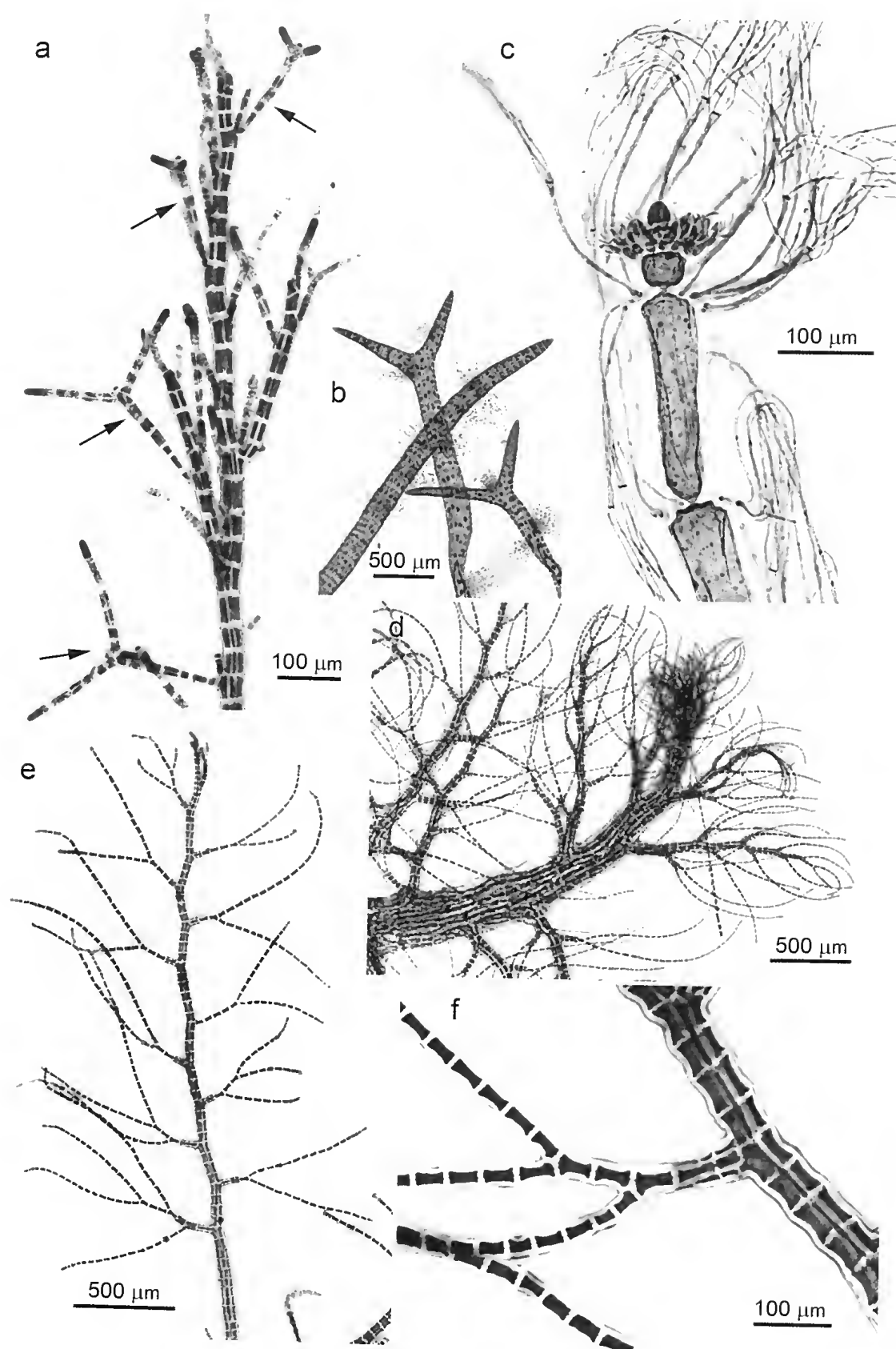


Figure 5. Phaeophyceae (a, b) and Rhodophyta (c–f). a. *Sphacelaria rigidula*, thallus habit with propagules (arrows). b. *Dictyota furcellata*, branch apices with surface hair clusters. c. *Anotrichium tenue*, branch apex showing whorled trichoblasts (colourless hairs). d. *Bostrychia flagellifera*, thallus habit with corticated primary axes tapering to uniseriate filaments. e, f. *Bostrychia moritziana*. e. thallus habit. f. detail showing uncorticated axes.

- 21 Branch apices blunt or with a sunken pit; pericentral cells persistent throughout thallus; spermatangia in plate-like structures 36. *Choudria succuleuta*
- 21: Branch apices with a distinctly sunken pit; pericentral cells only obvious near branch apices; spermatangia not in plate-like structures 45. *Laureucia* sp.
- 22 Axes with 4 pericentral cells 23
- 22: Axes with more than 4 pericentral cells 24
- 23 Attachment rhizoids in open connection with bearing cell, thallus primarily prostrate 47. *Polysiphonia scopulorum*
- 23: Attachment rhizoids pit-connected to bearing cell, thallus primarily upright .. 46. *Polysiphonia infestans*
- 24 Thallus with extensive prostrate axes; with 6 pericentral cells throughout; attachment rhizoids in open connection with bearing cell 48. *Polysiphonia teges*
- 24: Thallus primarily upright; with 6 pericentral cells in primary axes, 5 pericentral cells in lateral branches; attachment rhizoids cut off from bearing cell 49. *Polysiphonia* sp.
- 25 Thallus with nodal cortication only 40. *Gayliella fimbriata*
- 25: Thallus with complete cortication at least in part 23
- 26 Cortication complete on primary axes, but nodal on lateral branches .. 50. *Spyridia filamentosa*
- 26: Cortication complete throughout 35. *Centroceras* sp.

25. *Aglaothamnion cordatum* (Børgesen) Feldm.-Maz. 1941: 459.

Thallus small, to 15 mm tall, uncorticated, alternately branched with a single lateral branch per axial cell, attached by a cluster of rhizoidal cells. Lower cells of primary axes 100–140 µm diam., often with L:B c. 1, occasionally more elongate. Mid-thallus cells 140–180 µm long and 50–80 µm diam., tapering to upper elongate cells 7–10 µm diam., occasionally with terminal hairs. Tetrasporangia on distal region of lateral branch cells, ellipsoidal, 40–45 × 30–35 µm, tetrahedrally divided.

Specimen: Little Lagoon, epiphytic on *Bostrychia tenella*, 6 June 2009, J.M.Huisman (PERTH 08578230).

The Shark Bay specimen was tetrasporangial and other reproductive structures were not observed. Without the carposporophyte generation the species is difficult to distinguish from *Seirospora orientalis*, but in *Aglaothamnion cordatum* the tetrasporangia are slightly smaller than those of *Seirospora*, and are ellipsoidal rather than spherical when mature.

26. *Anotrichium tenue* (C.Agardh) Nägeli 1862: 399.

Thallus tufted, with spreading prostrate axes attached by mostly unicellular rhizoids, with sparingly branched erect axes to 5 mm tall growing from the proximal ends of cells. Trichoblasts in whorls at apices, dichotomously to polychotomously divided. Cells of prostrate axes 170–200 µm diam. [L:B 2.5–3]; cells of erect axes of similar diameter, but shorter distally [L:B 1–1.5]. Reproductive structures not observed (Fig. 5c).

Specimen: Little Lagoon, 6 June 2009, J.M.Huisman (PERTH 08578257).

27. *Bostrychia flagellifera* E.Post 1936: 34.

Thallus prostrate with dense lateral branches, robust, mat-forming, dull purple to deep red. Primary axes 150–250 µm diam., bearing alternate lateral branches every 2–3 axial cells. Lateral branches polysiphonous proximally, 70–100 µm diam., bearing ultimate uniseriate branches 15–30 µm diam., these tapering distally with cells L:B 1–1.5 (Figs 2g, 5d).

Specimen: Blind Inlet, South Passage, 11 June 2009, J.M.Huisman (PERTH 08578303)

This species, described originally from the Paramatta River in New South Wales, is also known from New Zealand and Japan (Post 1961). King & Puttock (in King *et al.* 1988) treat it as a subspecies of *Bostrychia tenella*, and a previous Shark Bay record was under that name (Kendrick *et al.* 1990). Recognition at species level was recommended by Zuccarello & West (2006) based on molecular analyses that showed *B. flagellifera* did not group with *B. tenella*, and the taxon displays a diagnostic synapomorphy (branching interval).

28. *Bostrychia moritziana* (Sond. ex Kütz.) J.Agardh 1863: 862

Thallus prostrate, mat-forming, purple to brown; main axes indeterminate, 20–40 (–60) mm long, bearing determinate lateral branches 2–3 mm long, with 1–3 orders of alternate branching; 2 tiers of pericentral cells per axial cell with 4–5 (–8) pericentral cells per tier around the main axes and primary lateral branches; ecorticate throughout; polysiphonous except for monosiphonous ultimate and penultimate determinate branches. Indeterminate axes 60–100 µm diam.; branches arising subdichotomously at intervals of more than 10 axial cells; determinate branches arising laterally at intervals of 2–5 (–8) axial cells. (Figs 5e, f).

Specimen: Long Tom Bay, South Passage, 11 June 2009, J.M.Huisman (PERTH 08578435)

Recorded from Steep Point, Shark Bay (26°08'S., 113°10'E., iii.1986, Wells UNSW 16271) by King & Puttock (1989: 32)

29. *Bostrychia radicaus* (Mont.) Mont. 1842: 661

Thallus prostrate with suberect branches, robust, turf-forming, purple to brown; main axes indeterminate, 10–15 (–20) mm long, bearing determinate lateral branches 2–3 mm long, with 1–2 (–3) orders of alternate branching; 2 tiers of pericentral cells per axial cell, with (5–) 7–8 pericentral cells per tier around the main axes and lateral branches, ecorticate and polysiphonous throughout; attached to the substratum by cladohaptera. Indeterminate axes 120–200 µm diam.; branches arising subdichotomously at intervals of more than 10 axial cells; determinate branches arising laterally at intervals (2–) 4–6 axial cells (Fig. 6a).

Specimen: Uendoo Creek, 4 June 2009, J.M.Huisman (PERTH 08578516); also recorded from Steep Point, Shark Bay (26°08'S., 113°10'E., iii.1986, Wells UNSW 16269) by King & Puttock (1989: 32).

30. *Bostrychia tenella* (J.V.Lamour.) J.Agardh 1863: 869.

Thallus prostrate with dense lateral branches, robust,

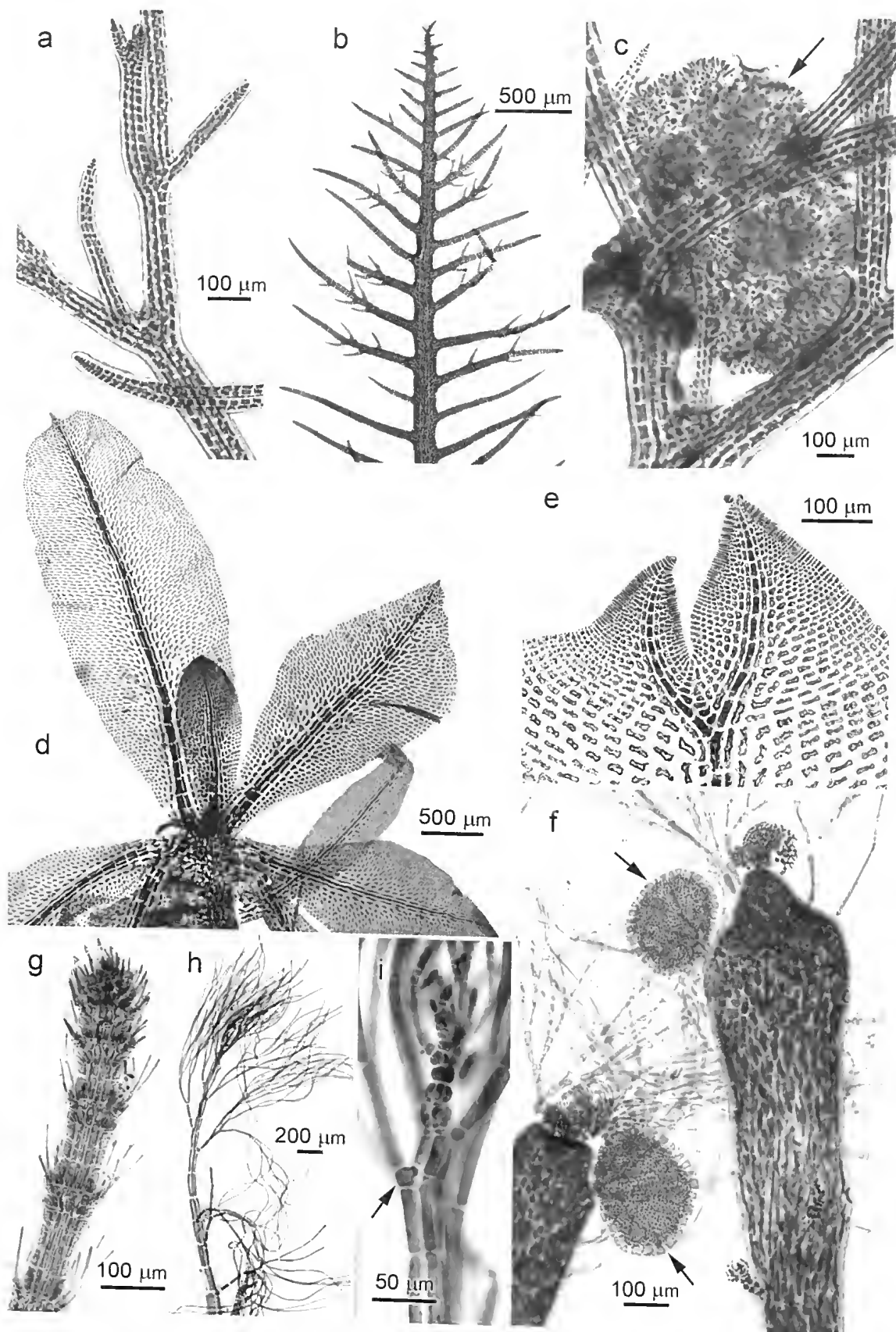


Figure 6. Rhodophyta. a. *Bostrychia radicans*, branch detail showing polysiphonous axes throughout. b. *Bostrychia tenella*, with regular alternate branches. c. *Bostrychiocolax australis* (arrow), forming a parasitic pustule on *Bostrychia radicans*. d. *Caloglossa leprieurii*, leafy branches with a distinct midrib. e. *Caloglossa monosticha*, branch apices with plate-like spermatangial branches (arrows). f. *Chondria succulenta*, Thallus habit with polysiphonous main axis and pigment monosiphonous laterals. g. *Centroceras* sp., detail of upper axis. h, i. *Dasya kristeninae*. h. basal cells of pigmented laterals (arrow). i. Detail of apex, showing quadrate basal cells of pigmented laterals (arrow).

mat-forming, dull purple, violet to brown; main axes indeterminate, 20–50 mm long, bearing determinate branches 2–3 mm long, with 1–3 (–4) orders of alternate branching; 2 tiers of 5–7 (–8) pericentral cells per axial cell; indeterminate axes and first-order lateral branches corticate; polysiphonous except for wholly or partially monosiphonous ultimate branches. Indeterminate axes 80–500 µm diam.; branches arising subdichotomously or laterally at intervals of 1 (–4) axial cells. Determinate branches arising at intervals of 1 (–2) axial cells. Tetrasporangial stichidia on ultimate lateral branches (Fig. 6b).

Specimen: Little Lagoon, 6 June 2009, J.M.Huisman (PERTH 08578249).

31. *Bostrychiocolax australis* Zuccarello & J.A.West 1994: 138.*

Thallus forming colourless irregularly shaped to hemispherical pustules laterally on host branches, to 600 µm tall and 900 µm broad. Structure filamentous, multiaxial, with darkly staining large internal cells bearing numerous radiating branches. Tetrasporangia terminal on filaments, ellipsoidal to obovoid, 20–30 µm long, 12–17 µm diam., tetrahedrally divided (Fig. 6c).

Specimen: Uendoo Creek, on *Bostrychia radicans* epiphytic on *Avicennia marina* pneumatophores, 4 June 2009, J.M.Huisman (PERTH 08578508).

This species is a parasitic red alga seemingly restricted to the host *Bostrychia radicans*. Two specimens were collected from the Uendoo Creek site, one male gametophyte and one tetrasporophyte. This represents a new generic record for Western Australia, the genus previously known only from Queensland (Zuccarello & West 1994: 138)

32. *Caloglossa lepriurii* (Mont.) G.Martens 1869: 234, 237.

Thallus forming low mats composed of arching leaf-like blades, pale brown to reddish brown, epiphytic and epilithic, loosely attached to the substratum at intervals by clusters of coalescent rhizoids arising from cortical pads produced by pericentral cells at the nodes; mature blades linear to suborbicular, (0.35–) 0.6–2.1 (–3.5) mm wide, with (0.8–) 3.1–6.2 (–7.5) mm between weakly to strongly constricted nodes, occasionally arising as stipitate rosettes; endogenous branches produced by an axial cell above the nodes; adventitious branches absent. Reproductive structures not observed (Fig. 6d).

Specimen: Wooramel, 5 June 2009, J.M.Huisman (PERTH 08578524); Faure I., 10 June 2009, J.M.Huisman (PERTH); also recorded from Shark Bay by West *et al.* 2001

33. *Caloglossa monosticha* M.Kamiya in M.Kamiya, J.Tanaka & Y.Hara 1997: 105.

Thalli forming low mats composed of arching blades, pale brown to olive-green, epiphytic, subdichotomously branched, loosely attached to the substratum at intervals by clusters of divergent rhizoids arising directly from nodal pericentral cells; mature blades linear to narrowly elliptical, 0.3–1.4 mm wide with 1.3–5.8 mm between slightly constricted nodes; stipes absent. Nodes on main

axes with all second- and third-order cell rows on the adjacent and opposite sides reaching the blade margin. Rhizoids arising from first and second adjacent and adaxial lateral pericentral (second-order) cells above the node, 6–10 cells and 0.6–1.5 mm long, 25–45 µm diam. Reproductive structures not observed (Fig. 6e).

Specimen: Dubaut Creek, 8 June 2009, J.M.Huisman (PERTH 08578354); also recorded from Monkey Mia, Shark Bay, by West *et al.* (2001: 192).

Caloglossa monosticha can be distinguished from *C. lepriurii* by the attachment rhizoids remaining free and not forming a stipe. This feature is best observed in well-developed specimens, as rhizoids in young branches of *C. lepriurii* are also free. A further distinction can be seen in the cell arrangement at nodes. In *C. lepriurii* the basal axial cell of the lateral branch lacks an adaxial pericentral cell, whereas these are present in *C. monosticha*. Wynne & De Clerck (1999) proposed that *C. monosticha* was conspecific with the earlier described *C. saigonensis* Tak.Tanaka & P.H.Hô, but this was rejected by Kamiya *et al.* (2003) based on molecular and culture studies.

34. *Catenella nipae* Zanardini 1872: 143.*

Thallus dark red to brown, to 4 cm tall, tufted or tangled, with sprawling terete stolons to 0.5 mm wide, attached at several points. Erect axes richly branched, segmented; segments elongate-ovoid, 3–5 mm long, 0.5–1.0 mm wide. Structure with a prominent apical cell but usually lacking a single distinct axial filament; centre of the medulla occupied by several longitudinal filaments, each with a single lateral filament, these forming a reticulate medulla of regularly spaced branched filaments 10–25 µm diam., often with stellate cells. Secondary connections between medullary filaments common. Cortex of 2 cell layers; inner layer of clavate to spherical cells; outer layer of ellipsoidal to elongate cells 3.5–7.0 µm diam., forming a palisade. Spermatangia in sori on thallus surface. Other reproduction not observed (Figs 7a, b).

Specimen: Uendoo Creek, 4 June 2009, J.M.Huisman (PERTH 08578532).

The present specimens agree in most respects with the description by Min-Thein & Womersley (1976), excluding the presence of two periaxial cells per axial cell, a feature regarded as characteristic for the genus (Guiry & Guiry, 2014). Later, however, Womersley (1994), described only one periaxial cell per axial cell. The primary axial filament in the Shark Bay specimens was often conspicuous, particularly so in material stained with aniline blue, this also differing from Womersley's description who suggested that the axial filament was inconspicuous. The persistent visibility of the axial filament is a feature of the closely related *Caulacanthus ustulatus*, but that species is not constricted. One of the specimens was male, with spermatangia produced in sori on the thallus surface.

35. *Centroceras* sp.*

Thallus with prostrate and assurgent axes, light red, to 3.5 mm tall, sparsely subdichotomously branched every c. 8 cells, but often with long unbranched axes. Prostrate axes attached by multicellular rhizoids arising 1–3 per

node from periaxial cells, basally as an extension of the periaxial cell and the first cross wall external to the node. Upright axes with forcipate apices. Segments 70–90 µm diam. [L:B < 1 near apices, to 5 in mature segments]. Periaxial cells 8–11 per node, each bearing 2 acropetal and 1 basipetal initials. First acropetal initial bearing either a spine or a gland cell, and 1 or 2 conical to elongate cells, these often forming elongate hairs. Second acropetal initial bearing 1 acropetal conical to elongate cell and a basipetal cortical filament. Basipetal initial bearing 1 basipetal cortical filament. Spines 2-celled (not including acropetal initial), in whorls of 4–6 per node. Gland cells ellipsoidal, 10–12 µm long, 7–10 µm diam. Basipetal cortical filaments 10–12 cells long, completely covering the axial cells, with cells of varying lengths, these often becoming transversely aligned towards the proximal portion of each segment (Fig. 6g).

Specimen: Wooramel, 5 June 2009, J.M.Huisman (PERTH 08578397).

This is a new species, known also from Barrow Island, the Rowley Shoals, and Scott Reef, which is being formally described elsewhere (Huisman, in prep.).

36. *Chondria sncculenta* (J.Agardh) Falkenb. 1901: 205–206, pl. 22: figs. 22, 23.*

Thallus with several simple to 1–3 times branched axes arising from a common holdfast, to 6 mm tall. Axes terete, 0.25–0.6 mm diam., with blunt to sunken apices with emergent filaments. Epidermal cells elongate to ellipsoidal, 17–20 µm diam. L:B to 7. Tetrasporangia near apices, spherical, 50–75 µm diam., tetrahedrally divided. Spermatangia in discoid plates, to 450 µm broad, with a single row of sterile marginal cells (Fig. 6f).

Specimen: Little Lagoon, 6 June 2006, J.M.Huisman (PERTH 08578346).

Although of only a small stature, both male and tetrasporic specimens were collected. These agree for the most part with the description by Gordon-Mills & Womersley (534–537), differing only in the smaller size of the thallus and tetrasporangia. In both cases this is probably due to the plant maturity.

37. *Crouania* sp.

Thallus filamentous, uncorticated, with prostrate and erect branches. Erect branches c. 750 µm tall, with axial cells 10–15 µm diam., L:B 1.5–2, each axial cell bearing a whorl of 3 branches, these 2–3 cells long and dichotomously branched (in one instance trichotomous). Reproductive structures not observed.

Specimen: Wooramel South, epiphytic on *Bostrychia tenella*, 5 June 2009, J.M.Huisman (PERTH 08578389; PERTH 08578613).

These are immature specimens that cannot be identified to species.

38. *Dasya kristeniae* I.A.Abbott 1998: 105.*

Thallus red, 9 mm tall, attached by clumped pigmented cells arising from the basal region. Primary axis polysiphonous, terete, basally to 200 µm diam., tapering to 50 µm diam. near apices, with sympodial apical

growth and pericentral cells developing spirally. Primary axial cells each with 5 pericentral cells and a branched, pigmented monosiphonous lateral arising in a 2/5 spiral. Segments of primary axis elongate, L:B 2–4. Monosiphonous laterals to 1.5 mm long, monopodial, dichotomously branched every 1–2 cells, with elongate cells 10–20 µm diam., L:B 5–7. Reproductive structures not observed (Figs 6h, i).

Specimen: Little Lagoon, epiphytic on *Polysiphonia teges*, 6 June 2009, J.M.Huisman (PERTH 08578567).

This small species is attributed to *Dasya* based on the production of five pericentral cells, sympodial growth of primary axes, and branched, monosiphonous pigmented laterals arising on every segment in a 2/5 spiral. Unlike most species of the genus, however, the pigmented lateral branches divide monopodially, and thus do not have dichotomies wherein the two distal cells have a confluent lateral face (the 'inverse Y junction' described by Parsons 1975: 562). Although this was not described by Abbott (1998, 1999), her figures of *Dasya kristeniae* appear to show a similar arrangement. Abbott (1998) described *D. kristeniae* as having only four pericentral cells, but also as having monosiphonous laterals arising in a 2/5 spiral, which is incompatible with four pericentral cells. Coppejans & Millar (2000: 329) attributed completely ecorticate (except for small rhizoids at the very base) plants from Papua New Guinea to *D. kristeniae*, although they did not comment on the number of pericentral cells.

39. *Erythrotrichia carnea* (Dillwyn) J.Agardh 1883: 15.*

Thallus red to purple-red, with erect filaments to 3 mm tall, attached by a single basal cell that can be lobed. Filaments mostly simple, 15–20 µm diam. (including a thick gelatinous wall); cells 12–14 µm long [L:B 0.7–1]. Monosporangia subspherical, cut off by a curved wall.

Specimen: Cape Lesueur, epiphytic on *Gayliella fimbriata*, 7 June 2009, J.M.Huisman (PERTH 08578605).

E. carnea forms small, unbranched, uniseriate filaments, epiphytic on a variety of algae. It is a common and widespread species.

40. *Gayliella fimbriata* (Setch. & N.L.Gardner) T.O.Cho & S.M.Boo in T.O.Cho *et al.* 2008: 723.*

Thallus red to purple-red, with prostrate and erect axes to 7.5 mm long, attached by rhizoids arising from periaxial cells of lower axes. Erect axes subalternately branched every 4 or 5 cells in the primary axes and every 5–7 cells in lateral axes. Apices straight to curved, not circinate. Periaxial cells 6, each producing basipetally a transversely aligned cell that subsequently cuts off 1 or 2 cells by oblique divisions from the lower corners, and acropetally a pair of cells that divide several times. Cortical cell development more extensive in older nodes. Distal cells of nodes commonly with elongate or clavate gland cells. Reproductive structures not observed (Fig. 7c).

Specimen: Cape Lesueur, 7 June 2009, J.M.Huisman (PERTH 08578362).

The genus *Gayliella* was erected by Cho *et al.* (2008) for several species previously placed in *Ceramium*, but which

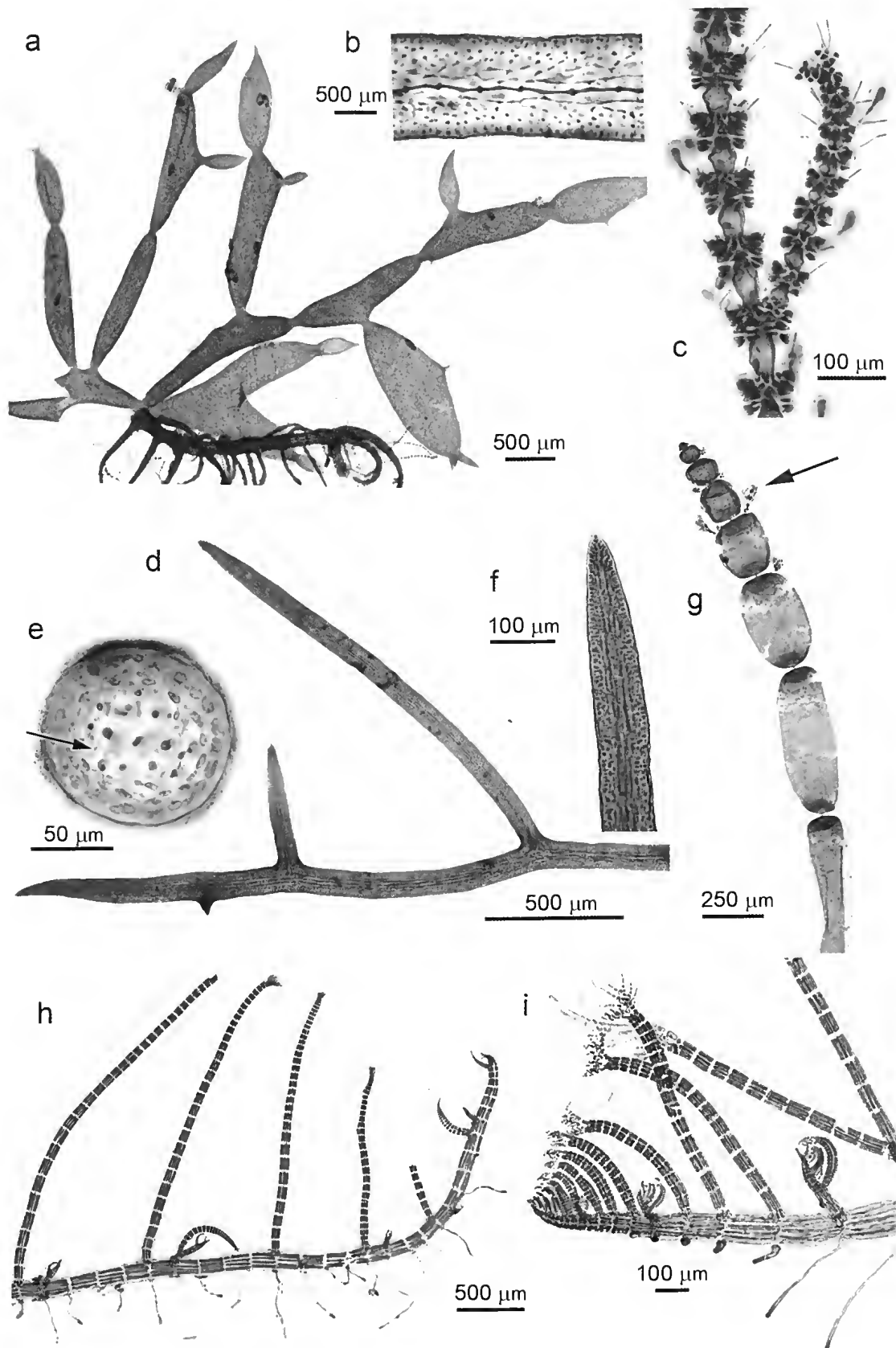


Figure 7. Rhodophyta. a, b. *Catenella nipae*. a. habit showing characteristic segmented thallus. b. showing obvious central axis. c. *Gayliella fimbriata*, detail of thallus showing filamentous construction with nodal cortication. d–f. *Gelidium minusculum*. d. Plant habit showing prostrate axis and simple upright axes. e. Transverse section of thallus showing rhizines at the medulla/cortex interface (arrow). f. Closer view of thallus showing pointed apex with a single apical cell. g. *Griffithsia heteromorpha*, habit. Note trichoblasts on upper cells (arrow). h. *Herposiphonia pacifica*, habit, showing prostrate axis with a simple determinate branch proximal to an indeterminate branch. i. *Herposiphonia tenella*, habit, showing regular pattern of three determinate branches and one indeterminate branch.

resolved in a segregate clade in molecular analyses and differed in having transversely aligned basipetal cortical cells. Prior to this, *Gayliella fimbriata* (as *Ceramium*) was one of several species thought to belong to a widespread, morphologically variable species *Ceramium flaccidum* (nov. *Gayliella flaccida*) (Womersley 1978). Thus many records of the latter, including those from Shark Bay (Huisman *et al.* 1990: 96; Kendrick *et al.* 1990: 51) are possibly incorrect and should be re-assessed.

41. *Gelidium minusculum* (Weber Bosse) R.E.Norris 1992: 17.*

Thallus forming creeping prostrate axes attached by clustered rhizoids, bearing sparse, perpendicular erect axes approximately every 500–700 µm, although these often more frequent or absent for long distances. Prostrate axes terete, to 150 µm diam. Upright axes terete, to 1–4 mm tall, 80–100 µm diam., mostly simple, with pointed apices. Structure uniaxial, when mature with a medulla of longitudinal filaments, these cross-linked by pit-connections, and a cortex of 2–4 layers of smaller pigmented cells. Outer cells rounded to transversely elongate in surface view, 12–18 µm long, 5–8 µm broad, in vague, meandering longitudinal lines. Rhizines inconspicuous, in small bundles at the medulla/cortex interface. Reproductive structures not observed (Figs 7d–f).

Specimen: Uendoo Creek, epiphytic on *Avicennia marina* pneumatophores, 4 June 2009, J.M.Huisman (PERTH 08578656).

This small, wiry species with cylindrical branches was originally described (but not illustrated) based on specimens from Indonesia (Weber-van Bosse 1921: 226, as *Gelidium pusillum* var. *minuscula*). Hatta & Prud'homme van Reine (367, fig. 9A) illustrated a plant that was collected as a mangrove epiphyte from Sumba, Indonesia. The taxon was subsequently recorded from South Africa and raised to species level by Norris (1992), who regarded *G. pusillum* (*sensu stricto*) to be considerably more restricted in distribution than previously believed. A subsequent study by Millar & Freshwater (2005) supported this view of *G. pusillum*, but referred the South African taxon to *Gelidium isabelae* Taylor. The Shark Bay specimens have uniformly terete branches that are never flattened, similar to the mangrove epiphyte described by Hatta & Prud'homme van Reine (1991: 368, table 3), but differing from the lagoonal plants with spatulate upright branched described by those authors. Flattening of branches in *Gelidium* often occurs when they become reproductive, however, and the Shark Bay specimens were vegetative only.

42. *Griffithsia heteromorpha* Kütz. 1863: 2, pl. 3, figs a, b.*

Thallus red, filamentous, 3.5 mm tall, attached by rhizoids and cells arising from lower cells. Lower cells cylindrical to clavate, 100–200 µm diam., L:B ±4, grading to upper barrel-shaped to spherical cells 200–250 µm diam., L:B ±1, then tapering to apical cells. Upper cells each with 2–3 distal trichoblasts. Reproductive structures not observed (Fig. 7g).

Specimen: Little Lagoon, epiphytic on *Centroceras* sp., 6 June 2006, J.M.Huisman (PERTH 08578338).

Griffithsia heteromorpha is similar in form to other species of the genus and is distinguished by its tetrasporangia lacking an involucre (protective branches). The present specimen is immature and lacks this feature, but morphologically accords with this common species.

43. *Herposiphonia pacifica* Hollenb. 1968b: 549.*

Thallus red, attached by unbranched unicellular rhizoids, with digitate tips arising from the distal end of ventral pericentral cells. Indeterminate prostrate axes with circinate apices, with indeterminate axes arising laterally on alternate sides every 3 or 4 segments. Determinate lateral branches arising dorsally every 3 segments, 1 segment proximal to the indeterminate lateral branch. Prostrate axes terete, 130–145 µm diam. [segment L:B c. 1], with 8–11 pericentral cells. Determinate branches initially curved but becoming straight, unbranched, to 35 segments long when mature, terete, 80–100 µm diam. [segment L:B mostly 1–1.5], with 8–11 pericentral cells. Determinate axes with well-developed apical trichoblasts to 1.6 mm long, dichotomously divided to 7 times. (Fig. 7h).

Specimen: Uendoo Creek, 4 June 2009, J.M.Huisman (PERTH 08578540).

44. *Herposiphonia tenella* (C.Agardh) Ambronn 1880: 197.

Thallus red, with prostrate indeterminate and erect determinate axes, attached by unbranched unicellular rhizoids arising from the distal end of ventral pericentral cells. Indeterminate prostrate axes with circinate apices, with a regular sequence of 3 determinate and 1 indeterminate lateral branches; determinate axes arising dorsally or dorso-laterally, but erect; indeterminate axes ventro-lateral and prostrate. Prostrate axes terete, 100–110 µm diam. [segment L:B c. 1], with 9 or 10 pericentral cells. Determinate branches initially curved but straightening, unbranched, 1.5–2.5 mm long, with 9–11 segments when mature, terete, 60–75 µm diam. [segment L:B mostly 1–4], with 6–9 pericentral cells. All axes with terminal trichoblasts, these dichotomously divided, with tapering unpigmented cells. Cells with numerous spherical plastids, these often pectinate (Fig. 7i).

Specimen: Cape Lesueur, 7 June 2009, J.M.Huisman (PERTH 08578788).

This species, the generitype, is often treated as a form of *Herposiphonia secunda* (C.Agardh) Ambronn (see Wynne 1985), but recent studies have regarded it as a distinct species (Schneider & Searles, 1997; Masuda & Kogame 2000). It is characterized by the regular sequence of determinate and indeterminate branches.

45. *Laurencia* sp.

Thallus with several simple to once-branched axes arising from a common holdfast, to 8 mm tall. Axes terete, 0.25–0.5 mm diam., with blunt apices and an apical pit with emergent filaments. Epidermal cells with longitudinal pit connections, in surface view rounded to ellipsoidal, 20–50 µm diam. Tetrasporangia with parallel arrangement near apices, spherical, 100–130 µm diam., tetrahedrally divided (Fig. 8a).

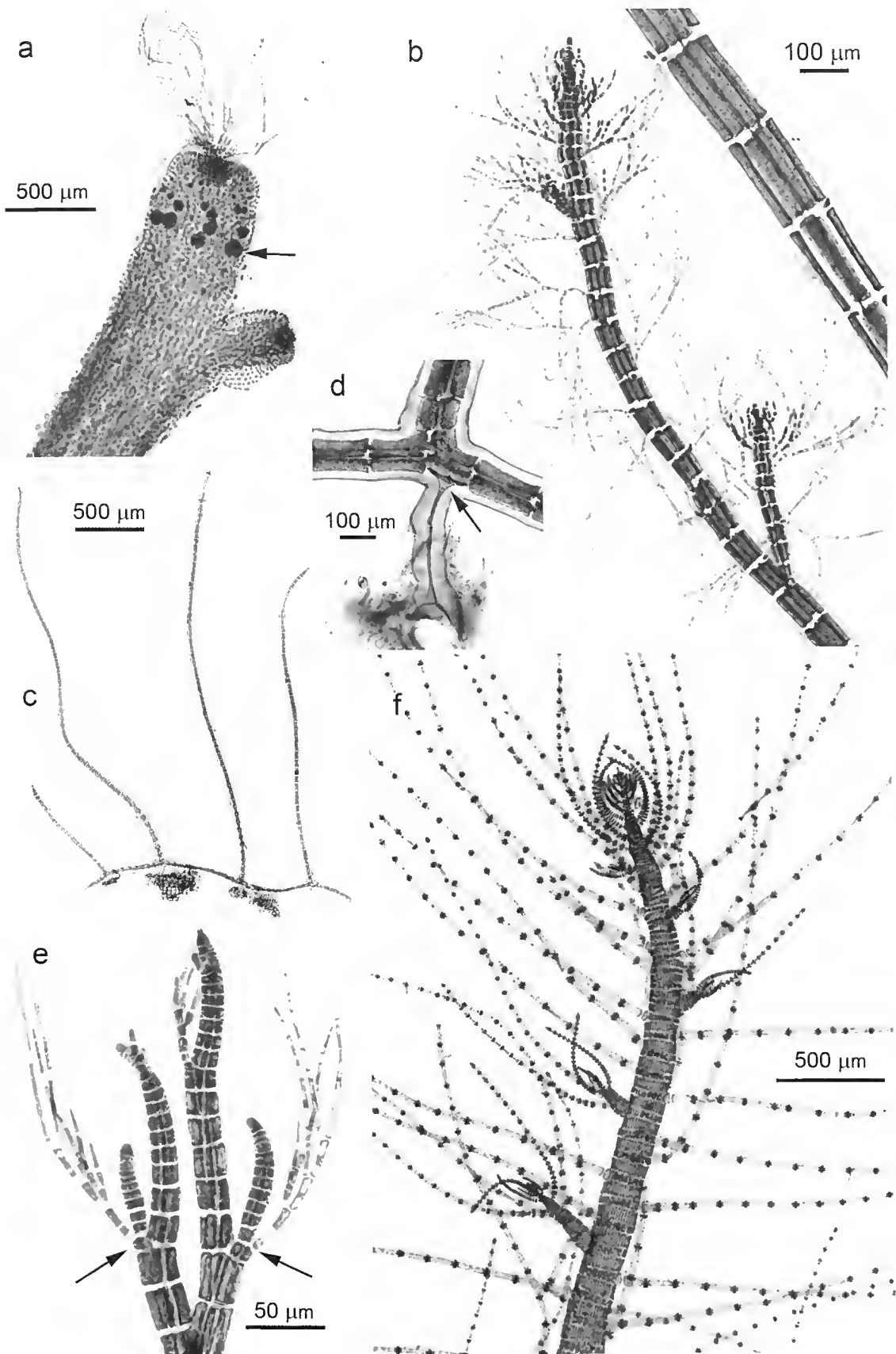


Figure 8. Rhodophyta. a. *Laurencia* sp., branch apex with tetrasporangia (arrow). b. *Polysiphonia infestans*, branch apex showing trichoblasts and (at right) a portion of an older branch, showing considerable variation in branch width. c, d. *Polysiphonia scopulorum*. c. Thallus habit, with prostrate axes and simple upright branches. d. Detail of attachment rhizoids in open connection with bearing cell (arrow). e. *Polysiphonia* sp., branch apices showing origin of lateral branches in axils of trichoblasts (arrows). f. *Spyridia filamentosa*, thallus habit, with fully corticated primary axis bearing lateral filaments corticated only at nodes.

Specimen: Little Lagoon, 6 June 2009, *J.M.Huisman* (PERTH 08578265).

These plants are reproductively mature but show few diagnostic features. They agree with *Laurencia intricata* J.V.Lamour. as described by Price & Scott (1992), but we defer specific placement until more luxuriant specimens are available.

46. *Polysiphonia infestans* Harv. 1855: 539.

Thallus red, primarily erect, to 16 mm tall, or with limited prostrate axes, attached to the substratum by unicellular digitate rhizoids arising from basal cells of primary axes. Erect axes subdichotomously branched every 5–10 segments. Axes with 4 pericentral cells and a trichoblast/scar cell on each segment in a spiral pattern with a 1/4 divergence between successive segments. Lower segments 390–430 µm diam. (including wall to 100 µm thick) [L:B 0.4–0.5 (c. 1 if the wall is excluded)]; mid-thallus segments 100–170 µm diam. [L:B 1–1.3 (–)], tapering gradually to upper segments 40–75 µm diam. [L:B 1–1.2]. Lateral branches replacing trichoblasts. Spermatangia in cylindrical to lanceolate heads forming as one branch of a basal dichotomy of trichoblasts, 170–290 µm long, 40–45 µm diam., without a sterile apical cell (Fig. 8b).

Specimen: Wooramel South, 5 June 2009, *J.M.Huisman* (PERTH); Faure I., 10 June 2009, *J.M.Huisman* (PERTH 08578311).

47. *Polysiphonia scopulorum* Harv. 1855: 540.

Thallus with well-developed prostrate axes, 80–100 µm diam., attached by unicellular rhizoids in open connection with bearing cell. Upright axes to 3 mm tall, often arising from segments adjacent to rhizoids, 50–100 µm diam., simple to sparsely branched, trichoblasts rudimentary at apices, soon deciduous. All axes with 4 pericentral cells. Scar cells occasionally present. Pericentral cells equidimensional near apices, forming segments L:B 0.3–0.5; lower segments L:B 0.8–1. Reproductive structures not observed (Figs 8c, d).

Specimen: Uendoo Creek, 4 June 2009, *J.M.Huisman* (PERTH). Little Lagoon, 6 June 2009, *J.M.Huisman* (PERTH 08578559).

The extensive prostrate axes, 4 pericentral cells per axial cell, and attachment rhizoids in open connection to the parent cell are characteristic of this species (Womersley 1979: 467–469). It is similar to *Polysiphonia teges* (see below), but that species has 6 pericentral cells.

48. *Polysiphonia teges* Womersley 1979: 494, fig. 10A–C.*

Thallus with prostrate axes, 90–100 µm diam., attached by unicellular rhizoids in open connection with bearing cell. Upright axes to 9 mm tall, 75–100 µm diam., sparsely branched, trichoblasts rudimentary at apices, soon deciduous. All axes with 6 pericentral cells, these generally slightly rounded. Scar cells occasionally present. Segment L:B generally ≤ 1, rarely longer. Reproductive structures not observed.

Specimen: Little Lagoon, 6 June 2009, *J.M.Huisman* (PERTH 08578621).

49. *Polysiphonia* sp.*

Thallus 32 mm tall, mostly upright, attached by thin rhizoids arising from pericentral cells near base. Axes 300–350 µm diam. near base, segment L:B ±0.6, tapering gradually to mid thallus 150 µm diam., L:B ±1, then to upper branches 50 µm diam., L:B 2–2.5. Axes with 6 pericentral cells in primary axes, 5 pericentral cells in lateral branches and minor axes. Trichoblasts present near apices, 300–600 µm long, 2–3 times subdichotomously divided, with hyaline cells. Lateral branches arising every 7–15 segments, initially in axils of trichoblasts, slightly narrowed at branch base. Scar cells at intervals of 2–6 segments, occasionally at regular intervals of 3 or 4. Reproductive structures not observed (Fig. 8e).

Specimen: Wooramel central, 5 June 2009, *J.M.Huisman* (PERTH 08578818).

This specimen possibly represents a new species. The combination of 5–6 pericentral cells, lateral branches arising in association with trichoblasts, and the irregular occurrence of scar cells does not appear to have been described previously, certainly not for any species recorded for Australia (Cribb 1983; Price & Scott 1992; Womersley 1979). It appears to be similar to *Polysiphonia homoia*, a species described originally from Isla Guadalupe, Mexico (Setchell & Gardner 1930), but since recorded from several other tropical locations in the Pacific (Hollenberg 1968a, Abbott 1999, N'Yeurt & Payri 2010). Hollenberg commented on some important differences between his material and the type, which suggests that more than one taxon might be involved. Setchell & Gardner (1930: 162) stated that *P. homoia* was 'constantly 5-siphonous' (i.e. with 5 pericentral cells), which differs from the Shark Bay specimen which had 6 pericentral cells in major axes. Unfortunately reproductive specimens were not collected and we defer any taxonomic decisions until additional material is available.

50. *Spyridia filamentosa* (Wulfen) Harv. 1833: 337.

Thallus to 10 cm tall. Growth from a prominent apical cell, producing a series of short cells before initiation of nodal cortication. Determinate or indeterminate lateral branches arising singly from each axial cell in a spiral pattern, or adventitiously from cortical cells. Primary axes with a ring of 10–14 cells at the nodes, these dividing basipetally to form a ring of longitudinally elongate cells covering the internodal region. Primary axes thus with alternating bands of broad and narrow cells, later mixed with corticating rhizoids. Determinate laterals 20–25 cells long, initially with short cells and attaining full cell number before producing nodal cortication, often with a terminal spinous cell but this generally lost. Mature determinate branches 1.5–2.0 mm long, with cells 30–55 µm wide [L:B to 4–5], and nodal cortication of 6–8 cells, these dividing to form a band of 1 or 2 (rarely 3) layers. Tetrasporangia arising singly or in sequentially maturing pairs on the adaxial surface of determinate branch nodal cells, sessile, pyriform when young but becoming spherical, 60–72 µm diam. (including wall 10–12 µm thick), tetrahedrally divided. Other reproductive structures not observed (Fig. 8f).

Specimen: Faure I., 10 June 2009, *J.M.Huisman* (PERTH 08578281).

51. *Stylonema alsidii* (Zanardini) K.M.Drew 1956: 72.*

Thallus erect, usually epiphytic, inconspicuous, to 500 µm tall, pseudofilamentous, branched, uniseriate. Cells within a conspicuous mucilaginous sheath, 15–25 µm diam., this often not obvious near the apices but conspicuous near the base and 2–3 times the diameter of the cells; cells 7–10 µm diam. [L:B 0.5–2.0], mostly cylindrical, but basal cells of branches tapering proximally.

Specimen: Wooramel, epiphytic on *Acetabularia peniculus*, 5 June 2009, J.M.Huisman (PERTH 08578729).

A small, uniseriate epiphyte, possibly more widespread than the present records indicate.

DISCUSSION

The present account records 51 species of marine algae and cyanobacteria from the pneumatophores of the mangrove *Avicennia marina* in Shark Bay, Western Australia. Of these, the vast majority (31) represent new records for the bay, with three species also newly recorded for Western Australia. These observations most likely reflect the relative paucity of collections from the region, and are not indicative of newly introduced species. The macroalgae of Shark Bay are represented in the Western Australian Herbarium (PERTH) by only 212 specimens, mostly collected by JMH or Gary Kendrick and Diana Walker as part of the University of Western Australia's research program in the 1980s. None of these specimens are mangrove epiphytes, and the group was similarly overlooked in the collation of records presented in Huisman *et al.* (1990). Thus the surfeit of new records presented here is to be expected following the initiation of interest in the region's mangrove-associated flora.

The range of taxa recorded is remarkably similar to that reported from mangals elsewhere in Australia (e.g. Saenger *et al.* 1977, Davey & Woelkerling 1980; Beanland & Woelkerling 1982; King & Wheeler 1985) and worldwide (e.g. Lambert *et al.* 1987; West 1991; Skelton & South 2002; West *et al.* 2013). The flora includes species of *Bostrychia*, *Caloglossa*, and *Catenella*, which, while none are obligate, are almost universally recorded as part of mangrove floras (King 1981). Other genera recorded for Shark Bay that were also recorded for N.S.W. mangroves by King & Wheeler (1985) include *Erythrotrichia*, *Polysiphonia*, *Spyridia*, *Sphacelaria*, *Chaetomorpha*, *Cladophora*, *Ulva*, *Rhizoclonium*, and *Gayralia* (as *Ulvaria*). These taxa, however, are commonly found as epiphytes on a range of seagrasses and larger macroalgae and are best considered as generalists.

Mangrove habitats are typically regarded as having a low diversity of epiphytes, and this was commented on by King (1981: 322), who suggested that these habitats are unfavourable due to a lack of stable substratum (excluding the mangroves), mud in suspension, and the physiological stress placed on algae in a situation of fluctuating salinity. King (1981: 322) also suggested that the "algal flora of marshes and mangals is depauperate and dull", resulting in little incentive for floristic studies. Despite this, King himself devoted much of his life to studying the mangrove algal flora, and phycologists such as John West (University of Melbourne) and Joe

Zuccarello (Victoria University of Wellington) have used molecular and culture studies to tease out the minutiae of the biology of mangrove epiphytes such as *Bostrychia* and *Caloglossa*, resulting in several landmark studies (e.g., Zuccarello & West 2006). Despite (or perhaps because of) the limited diversity of mangrove-associated algae, the group has been the subject of considerable interest and provided model organisms for life history and taxonomic studies.

The presence of 51 species at Shark Bay is comparable to the 32 recorded for N.S.W. by King & Wheeler (1985, not including cyanobacteria), 49 for South Australia by Beanland & Woelkerling (1982), and 22 species by Davey & Woelkerling (1980) for Victoria. While those diversity estimates might seem small in comparison to the corresponding local floras, the marine benthic flora of Shark Bay was given at only 153 species by Huisman *et al.* (1990), the low number undoubtedly an underestimate but also a clear reflection of the lack of hard substrata in the bay. Thus the mangrove community, with almost a quarter of the now known Shark Bay flora, represents a significant contributor to the bay's macroalgal diversity.

While this study aimed to document this algal community, we did notice marked differences in the diversity of algal flora at some sites, including some where the pneumatophores were essentially devoid of algae. The occurrence of species did not exhibit any consistent broad scale patterns across the study sites, and such differences may relate to site-specific factors like tree size and canopy density. As this study was essentially a qualitative snapshot of this community based on sampling over several days, it would be beneficial if further ecological research was undertaken to examine factors that influence the composition and distribution of this poorly known community.

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REFERENCES

- ABBOTT I A 1998. Some new species and new combinations of marine red algae from the Central Pacific. *Phycological Research* 46, 97–109.
- ABBOTT I A 1999. *Marine red algae of the Hawaiian Islands*. Bishop Museum Press, Honolulu, Hawaii.
- AGARDH C A 1817. *Synopsis algarum Scandinaviae, adjecta dispositione universali algarum*. Ex officina Berlingiana, Lundae [Lund].
- AGARDH J G 1848. *Species genera et ordines algarum, seu descriptiones succinctae specierum, generum et ordinum, quibus algarum regnum constituitur. Volumen Primum. Algas fucoidae complectens*. C.W.K. Gleerup, Lundae [Lund].
- AGARDH J G 1863. *Species genera et ordines algarum, seu descriptiones succinctae specierum, generum et ordinum, quibus algarum regnum constituitur. Volumen secundum: algas florideae complectens. Part 2, fasc. 3. pp. 787–1138, 1158–1291*. C.W.K. Gleerup, Lundae [Lund].

- AGARDH J G 1883. *Till algernes systematik. Nya bidrag. (Tredje afdelningen.)*. Lunds Universitets Års-Skrift, Afdelningen for Mathematik och Naturvetenskap 19(2), 1–177.
- AMBRONN H 1880. Über einige Fälle von Bilateralität bei den Florideen. *Botanische Zeitung* 38, 161–174, 177–185, 193–200, 209–216, 225–233, Plates III, IV.
- BEANLAND W R & WOELKERLING W J 1982. Studies on Australian mangrove algae: II. Composition and geographic distribution of communities in Spencer Gulf, South Australia. *Proceedings of the Royal Society of Victoria* 94, 89–106.
- BORNET É & FLAHAULT C 1886 '1887'. Revision des Nostocacées hétérocystées contenues dans les principaux herbiers de France. *Annales des Sciences Naturelles, Botanique, Septième série* 5, 51–129.
- BRUNNITT R K & POWELL C E 1992. Authors of Plant Names. A list of authors of scientific names of plants, with recommended standard forms of these names including abbreviations. Royal Botanic Gardens, Kew.
- CALM 1996. Shark Bay Marine Reserves Management Plan 1996–2006. Department of Conservation and Land Management, Perth, Western Australia.
- CHO T O, BOO S M, HOMMERSAND M H, MAGGS C A, MCIVOR L J & FREDERICO S 2008. *Gayliella* gen. nov. in the tribe Ceramieae (Ceramiales, Rhodophyta) based on molecular and morphological evidence. *Journal of Phycology* 44, 721–738.
- COPPEJANS E & MILLAR A J K 2000. Marine red algae from the North coast of Papua New Guinea. *Botanica Marina* 43, 315–346.
- CRIBB A B 1965. An ecological and taxonomic account of the algae of a semi-marine cavern, Paradise Cave, Queensland. *Papers from the Department of Botany University of Queensland* 4, 259–282.
- CRIBB A B 1983. *Marine algae of the southern Great Barrier Reef. Part 1. Rhodophyta*. Australian Coral Reef Society, Brisbane.
- DAVEY A & WOELKERLING W J 1980. Studies on Australian mangrove algae. I. Victorian communities; composition and geographic distribution. *Proceedings of the Royal Society of Victoria* 91, 53–66.
- DEH 2006. A guide to the integrated marine and coastal regionalization of Australia. IMCRA v4.0. Department of Environment and Heritage, Hobart.
- DREW K M 1956. *Conferva ceramicola* Lyngbye. *Botanisk Tidsskrift* 53, 67–74.
- FALKENBERG P 1901. Die Rhodomelaceen des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. *Fauna und Flora des Golfes von Neapel, Monographie* 26. pp. i–xvi, 1–754, 10 figs, 24 pls. Berlin.
- FELDMANN-MAZOYER G 1941 '1940'. *Recherches sur les Céramiacées de la Méditerranée occidentale*. Imprimerie Minerva, Alger.
- FORTI A 1907. *Sylloge algarum omnium hucusque cognitarum. Vol. V. Sylloge Myxophycearum*. Sumptibus auctoris, Patavii [Padova].
- GEPP A & GEPP E S 1911. The Codiaceae of the Siboga Expedition including a monograph of Flabellariaceae and Udoteae. *Siboga-Expedition Monographie* LXII. E.J. Brill, Leiden.
- GOMONT M 1892 '1893'. Monographie des Oscillariées (Nostocacées Homocystées). Deuxième partie. – Lyngbyées. *Annales des Sciences Naturelles, Botanique, Série 7* 16, 91–264, pls 1–7.
- GORDON-MILLS E M & WOMERSLEY H B S 1987. The genus *Chondria* C. Agardh (Rhodomelaceae, Rhodophyta) in southern Australia. *Australian Journal of Botany* 35, 477–565.
- GUIRY M D & GUIRY G M 2014. AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. <http://www.algaebase.org>; searched on 18 August 2014.
- HARVEY W H 1833. Div. II. Confervoideae; Div. III. Gloiocladeae. In: *The English Flora of Sir James Edward Smith. Class XXIV. Cryptogamia*. Vol. V. (or Vol. II of Dr. Hooker's British flora). Part I. Comprising the Mosses, Hepaticae, Lichens, Characeae and Algae. (ed. W J Hooker). Longman, Brown, Green & Longmans Paternoster-Row, London, 263–265, 265–266, 326–389, 389–405.
- HARVEY W H 1849. *Phycologia britannica, or, a history of British sea-weeds: containing coloured figures, generic and specific characters, synonymes, and descriptions of all the species of algae inhabiting the shores of the British Islands*. Reeve & Benham, London.
- HARVEY W H 1855. Some account of the marine botany of the colony of western Australia. *Transactions of the Royal Irish Academy* 22, 525–566.
- HATTA A M & PRUD'HONIME VAN REINE W F 1991. A taxonomic revision of Indonesian Gelidiales (Rhodophyta). *Blumea* 35, 347–380.
- HOEK C. VAN DEN 1963. *Revision of the European species of Cladophora*. Proefschrift...Rijksuniversiteit te Leiden. E. J. Brill, Leiden.
- HOFFMANN L 1992. Marine Cyanophyceae of Papua New Guinea IV. New Chroococcales. *Belgian Journal of Botany* 125, 29–32.
- HOLLENBERG G J 1968a. An account of the species of *Polysiphonia* of the central and western tropical Pacific Ocean. II. *Polysiphonia*. *Pacific Science* 22, 198–207.
- HOLLENBERG G J 1968b. An account of the species of the red alga *Herposiphonia* of the central and western tropical Pacific Ocean. *Pacific Science* 22, 536–559.
- HUISMAN J M, KENDRICK G A, WALKER D I & COUTÉ A 1990. The Marine Algae of Shark Bay, Western Australia. In: Berry P F, Bradshaw S D & Wilson B R (eds) *Research in Shark Bay – Report of the France-Australe Bicentenary Expedition Committee*, pp. 89–100. Western Australian Museum, Perth.
- HUISMAN J M, KENDRICK A J & RULE M J 2011. Benthic algae and seagrasses of the Walpole and Nornalup Inlets Marine Park, Western Australia. *Journal of the Royal Society of Western Australia* 94, 29–44.
- KAMIYA M, TANAKA J & HARA Y 1997. Comparative morphology, crossability, and taxonomy within the *Caloglossa continua* (Delesseriaceae, Rhodophyta) complex from the western Pacific. *Journal of Phycology* 33, 97–105.
- KAMIYA M, ZUCCARELLO G C & WEST J A 2003. Evolutionary relationships of the genus *Caloglossa* (Delesseriaceae, Rhodophyta) inferred from large-subunit ribosomal RNA gene sequences, morphological evidence and reproductive compatibility, with description of a new species from Guatemala. *Phycologia* 42, 478–497.
- KENDRICK A J, HUISMAN J M & RULE M J 2009. *Marvellous Mangroves. Landscape. Summer edition 2009–2010*. Published by the Department of Environment and Conservation, Western Australia, pp. 50–56.
- KENDRICK G A, HUISMAN J M & WALKER D I 1990. Benthic marine algae in Shark Bay, Western Australia. *Botanica Marina* 33, 47–54.
- KING R J 1981. Mangroves and saltmarsh plants. In: *Marine Botany: an Australasian perspective*. (eds M N Clayton & R J King). Longman Cheshire, Melbourne, 308–328.
- KING R J & PUTTOCK C F 1989. Morphology and taxonomy of *Bostrychia* and *Stictosiphonia* (Rhodomelaceae / Rhodophyta). *Australian Systematic Botany* 2, 1–73.
- KING R J & PUTTOCK C F 1994a. Morphology and taxonomy of *Caloglossa* (Delesseriaceae, Rhodophyta). *Australian Systematic Botany* 7, 89–124.
- KING R J & PUTTOCK C F 1994b. Macroalgae associated with mangroves in Australia: Rhodophyta. *Botanica Marina* 37, 181–191.
- KING R J & WHEELER M 1985. Composition and geographic distribution of mangrove macroalgal communities in New South Wales. *Proceedings of the Linnean Society of New South Wales* 108, 97–117.
- KING R J & PUTTOCK C F & VICKERY R S 1988. A taxonomic study on the *Bostrychia tenella* complex (Rhodomelaceae, Rhodophyta). *Phycologia* 27, 10–19.

- KRAFT G T 2007. *Algae of Australia. Marine benthic algae of Lord Howe Island and the southern Great Barrier Reef, 1. Green algae.* Australian Biological Resources Study & CSIRO Publishing, Canberra & Melbourne.
- KÜTZING F T 1843. *Phycologia generalis oder Anatomie, Physiologie und Systemkunde der Tange.* F A Brockhaus, Leipzig.
- KÜTZING F T 1849. *Species algarum.* F.A. Brockhaus, Lipsiae [Leipzig].
- KÜTZING F T 1863. *Tabulae phycologicae; oder, Abbildungen der Tange.* Vol. XIII. Gedruckt auf kosten des Verfassers (in commission bei W Köhne), Nordhausen.
- LAMBERT G, STEINKE T D & NAIDOO Y 1987. Algae associated with mangroves in southern African estuaries. I. Rhodophyceae. *South African Journal of Botany* 53, 349–361.
- LELIAERT F & BOEDEKER C 2007. Cladophorales. In: Brodie J, Maggs C A & John D (eds) *Green seaweeds of Britain and Ireland*, pp. 131–183. The British Phycological Society.
- LITTLER D S & LITTLER M M 2000. *Caribbean reef plants. An identification guide to the reef plants of the Caribbean, Bahamas, Florida and Gulf of Mexico.* Offshore Graphics, Washington.
- LOGAN B W, HOFFMAN P & GEBELEIN C D 1974. Algal Mats, Cryptalgal Fabrics, and Structures, Hamelin Pool, Western Australia. In: Logan B W, Read J F, Hagan G M, Hoffman P, Brown R G, Woods P J & Gebelein C D (eds) *Evolution and Diagenesis of Quaternary Carbonate Sequences, Shark Bay, Western Australia.* American Association of Petroleum Geologists, Tulsa, Oklahoma, Memoir 22, 140–194.
- MARTENS G VON 1869. Beiträge zur Algen-Flora Indiens. *Flora* 52, 233–238.
- MASUDA M & KOGAME K 2000. *Herposiphonia elongata* sp. nov. and *H. tenella* (Rhodophyta, Ceramiales) from the western Pacific. *Cryptogamie, Algologie* 21, 177–189.
- MILLAR A J K & FRESHWATER D W 2005. Morphology and molecular phylogeny of the marine algal order Gelidiales (Rhodophyta) from New South Wales, including Lord Howe and Norfolk Islands. *Australian Systematic Botany* 18, 215–263.
- MIN-THIEN U & WOMERSLEY H B S 1976. Studies on southern Australian taxa of Solieriaceae, Rhabdoniaceae and Rhodophyllidaceae (Rhodophyta). *Australian Journal of Botany* 24, 1–166.
- MONTAGNE C 1842. *Bostrychia*. Dictionnaire Universel d'Histoire Naturelle [Orbigny] 2, 660–661.
- NÄGELI C 1862 '1861'. Beiträge zur morphologie und systematik der Ceramiales. *Sitzungsberichte der Königlichen Bayerischen Akademie der Wissenschaften zu München* 1861(2), 297–415.
- NIELSEN R, PETERSEN G, SEBERG O, DAUGBJERG N, O'KELLY C J & WYSOR B 2013. Revision of the genus *Ulvella* (Ulvellaceae, Ulvophyceae) based on morphology and tufA gene sequences of species in culture, with *Acrochaete* and *Pringsheimiella* placed in synonymy. *Phycologia* 52, 37–56.
- NORRIS R E 1992. The marine red algae of Natal, South Africa: order Gelidiales (Rhodophyta). *Memoirs of the Botanical Survey of South Africa* 61, 1–43.
- N'YEURT A D R & PAYRI C E 2010. Marine algal flora of French Polynesia III. Rhodophyta, with additions to the Phaeophyceae and Chlorophyta. *Cryptogamie, Algologie* 31, 3–205.
- PARSONS M J 1975. Morphology and taxonomy of the Dasyaceae and the Lophothaliaeae (Rhodomelaceae) of the Rhodophyta. *Australian Journal of Botany* 23, 549–713.
- PLAYFORD P E 1990. Geology of the Shark Bay area Western Australia. In: Berry P F, Bradshaw S D & Wilson B R (eds) *Research in Shark Bay: Report of the France-Australie Bicentenary Expedition Committee*, pp. 13–32. Western Australian Museum, Perth.
- POST E 1936. Systematische und pflanzengeographische Notizen zur *Bostrychia-Caloglossa*-Assoziation. *Revue Algologique* 9, 1–84.
- POST E 1961. *Bostrychia flagellifera* Post in Japan-A synoptic study. *Bulletin of the Research Council of Israel, Sect D Bot* 4, 101–115.
- PRICE I R & SCOTT F J 1992. *The turf algal flora of the Great Barrier Reef. Part I. Rhodophyta.* Botany Department, James Cook University, Townsville.
- QUOY J R C & GAIMARD P 1824. Zoologie. In: De Freycinet I (ed.) *Voyage autour du monde...sur les corvettes...l'Uranie et la Physicenne, pendant les années 1817, 1818, 1819 et 1829*, pp. i–vi, 1–713. Pilet Aine, Paris.
- REINKE J 1889. Algenflora der westlichen Ostsee deutschen Antheils. Eine systematisch-pflanzengeographische Studie. *Bericht der Kommission zur Wissenschaftlichen Untersuchung der deutschen Meere in Kiel* 6, [i–] iii–xi, 1–101.
- SAENGER P, SPECHT M, SPECHT L & CHAPMAN J 1977. Mangal and coastal salt marsh communities in Australasia. In: Chapman V J (ed.) *Wet coastal ecosystems*, pp. 293–345. Elsevier Scientific Pub. Co, Amsterdam.
- SCAGEL R F, GABRIELSON P W, GARBARY D J, GOLDEN L, HAWKES M W, LINDSTROM S C, OLIVEIRA J C & WIDDOWSON T B 1989. A synopsis of the benthic marine algae of British Columbia, southeast Alaska, Washington and Oregon. *Phycological Contributions, University of British Columbia* 3, vi + 532.
- SCHNEIDER C W & SEARLES R B 1997. Notes on the marine algae of the Bermudas. 2. Some Rhodophyta, including *Polysiphonia tongatensis* and a discussion on the *Herposiphonia secunda/tenella* complex. *Cryptogamie, Algologie* 1997, 187–210, 19 figs.
- SETCHELL W A & GARDNER N L 1930. Marine algae of the Revillagigedo Islands Expedition in 1925. *Proceedings of the California Academy of Science, Series 4* 19, 109–215.
- SIEGSMUND M A, JOHANSEN J R, KARSTEN U & FRIEDL T 2008. *Coleofasciculus* gen. nov. (Cyanobacteria): morphological and molecular criteria for revision of the genus *Microcoleus* Gomont. *Journal of Phycology* 44, 1572–1585.
- SKELTON P A & SOUTH G R 2002. Mangrove-associated Algae from Samoa, South Pacific. *Constancea* 83.12 (<http://ucjeps.berkeley.edu/constancea/83/>). Accessed 12 June 2014.
- SOLMS-LAUBACH H 1895. Monograph of the Acetabulariaceae. *Transactions of the Linnean Society of London, Second Series, Botany* 5, 1–39.
- TILDEN J E 1898 (1894–1909). *American Algae. Centuries I–VII, numbers 1–850.* Minneapolis, Minnesota.
- TRONO G C JR 1972 '1971'. Some new species of marine benthic algae from the Caroline Islands, western-central Pacific. *Micronesica* 7, 45–77.
- TSUDA R T, FISHER J R, VROOM P S & ABBOTT I A 2010. New records of subtidal benthic marine algae from Wake Atoll, Central Pacific. *Botanica Marina* 53, 19–29.
- WEBER-VAN BOSSE A 1921. *Liste des algues du Siboga. II. Rhodophyceae. Première partie. Protofloridae, Nemalionales, Cryptonemionales.* Vol. 59b, 187–310. Leiden.
- WEST J 1991. New algal records from the Singapore mangroves. *Gardens' Bulletin, Singapore* 43, 19–21.
- WEST J A, KAMIYA M, LOISEAUX DE GOER S, KARSTEN U & ZUCCARELLO G C 2013. Observations on some mangrove-associated algae from the western Pacific (Guam, Chuuk, Kosrae, & Pohnpei). *Algae* 28, 241–266.
- WEST J A, ZUCCARELLO G C & KAMIYA M 2001. Reproductive patterns of *Caloglossa* species (Delesseriaceae, Rhodophyta) from Australia and New Zealand: multiple origins of asexuality in *C. lepreurii*. Literature review on apomixis, mixed-phase, bisexuality and sexual compatibility. *Phycological Research* 49, 183–200.
- WHITTON B A 2011. Cyanobacteria (Cyanophyta). In: John D M, Whitton B A & Brook A J (eds) *The freshwater algal flora of the British Isles. An identification guide to freshwater and terrestrial algae.* Second edition, pp. 31–158. Cambridge University Press, Cambridge.
- WOMERSLEY H B S 1978. Southern Australian species of *Ceramium* Roth (Rhodophyta). *Australian Journal of Botany* 29, 205–257.

- WOMERSLEY H B S 1979. Southern Australian species of *Polysiphonia* Greville (Rhodophyta). *Australian Journal of Botany* **27**, 459–528.
- WOMERSLEY H B S 1984. *The marine benthic flora of southern Australia. Part I*. Adelaide: Government Printer, South Australia.
- WOMERSLEY H B S 1994. *The marine benthic flora of southern Australia – Part IIIA – Bangiophyceae and Florideophyceae (Acrochaetales, Nemaliales, Gelidiales, Hildenbrandiales and Gigartinales sensu lato)*. Australian Biological Resources Study, Canberra.
- WULFEN F X 1803. *Cryptogama aquatica*. *Archives de Botanique* **3**, 1–64.
- WYNNE M J 1985. Notes on *Herposiphonia* (Rhodomelaceae, Rhodophyta) in South Africa, with a description of a new species. *Cryptogamie, Algologie* **5**, 167–177.
- WYNNE M J & DE CLERCK O 1999. Taxonomic notes on *Caloglossa monosticha* and *Caloglossa saigonensis* (Delesseriaceae, Rhodophyta). *Contributions from the University of Michigan Herbarium* **22**, 209–213.
- ZANARDINI G 1872. *Phycearum indicarum pugillus a Cl. Eduardo Beccari ad Borneum, Sincapoore et Ceylanum annis MDCCCLXV-VI-VII collectarum quas cognitae determinavit, novasque descripsit iconibusque illustrare curavit Joannes Zanardini*. *Memorie del Reale Istituto Veneto di Scienze, Lettere ed Arti* **17**, 129–170.
- ZUCCARELLO G C & WEST J A 1994. Comparative development of the red algal parasites *Bostrychiocolax australis* gen. et sp. nov. and *Dawsoniocolax bostrychia* (Choreocolacaceae, Rhodophyta). *Journal of Phycology* **30**, 137–146.
- ZUCCARELLO G C & WEST J A 2006. Molecular phylogeny of the subfamily Bostrychioideae (Ceramiales, Rhodophyta); subsuming *Stictosiphonia* and highlighting polyphyly in species of *Bostrychia*. *Phycologia* **45**, 24–36.

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Aquatic invertebrate communities of wetlands along the Jurien coast of Western Australia

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Wetlands are a prominent feature of the coastal strip north and south of Jurien Bay. However, assessment of their conservation values and their vulnerability to anthropogenic disturbance is hampered by a lack of knowledge about their biotas. In spring 2011 a survey of aquatic invertebrates was undertaken to provide data that could be used to assess 1) potential effects of expanded gypsum mining in the region's salt lakes and 2) the dependence of the fauna on groundwater as a contribution to water resource planning. The survey collected 194 species, bringing the total number of species known from this area to 215. The fauna was dominated by species that are widespread in at least south-western Australia, with very few rare or restricted species. Community structure was strongly correlated with salinity, ionic composition, aquatic plant cover, organic litter and colour. The salt lakes had heterogeneous faunas and may be an important refuge for the endemic brine shrimp *Parartemia extracta*. In a region in which most wetlands are saline and/or ephemeral, the springs represent an important ecological refuge from drought for a large proportion of the fauna. However, there was little evidence of a groundwater-adapted fauna at the springs and there were few epigeal species known to be associated with groundwater discharge.

KEYWORDS: aquatic invertebrates, conservation, springs, Western Australia, wetlands

INTRODUCTION

Extending north and south of Jurien Bay, along the mid-west coast of Western Australia, lies one of a number of complexes of mostly saline coastal wetlands located between Holocene dunes of the Perth Basin (Figure 1). Other such systems include the Hutt Lagoon wetlands (Pinder *et al.* 2012), the Yalgorup system (Hale & Butcher 2007) and the Cooloongup system (Conservation Commission of Western Australia *et al.* 2010). This region is hydrologically complex, reflected in the wide variety of wetland types present, including a series of partly connected saline playas and samphire flats known as the Leeman Lagoons, plus a variety of springs, vegetated swamps and a permanent anchialine lake (Lake Thetis). With human populations growing rapidly along this coast (Government of Western Australia 2012) planning for sustainable water resource utilisation is essential. At present there is very little information on epigeal aquatic biodiversity in this region and its relationships with water quality and quantity, other than a couple of wetlands sampled by Pinder *et al.* (2004) and Susac *et al.* (2009) and listings of ad-hoc aquatic invertebrate collections from surficial and subterranean karstic habitats (Susac 2007). There has also been some assessment of stygofauna from aquifers in the Jurien area (Biota Environmental Sciences 2002). This paper contributes to sustainable water resource planning by describing and assessing the conservation significance of the invertebrate faunas of wetlands in the region, including many that are groundwater dependant. Also underlying this survey was the need to investigate patterns in the biodiversity of the region's salt lakes to inform decisions about potential expansion of gypsum mining.

Study area

The study area (Fig. 1) occupies approximately 500 km² of the Quindalup and Spearwood dune systems between about Cervantes and Coolimba; part of the northern Swan Coastal Plain which extends from the ocean inland to the Gingin Scarp. The area straddles the northern tip of the Perth IBRA7 subregion SWA02 and the western extent of the Lesueur Sandplains IBRA7 subregion GES02 (*sensu* Commonwealth of Australia 2012). A large proportion of the study area lies within conservation estate, with the largest reserves being Beekeepers Nature Reserve (66277 ha), Southern Beekeepers Nature Reserve (10862 ha) and Lesueur National Park (27234 ha). The region's climate is "subtropical with distinctly dry summers" (Bureau of Meteorology's modified Koppen climate classification: http://www.bom.gov.au/climate/environ/other/koppen_explain.shtml#appendix1, accessed 11 June 2013), with average annual rainfall between 500 and 600 mm (< 50 mm in summer) and average annual evaporation about 2000 mm. Jurien Bay has an average annual maximum temperature of 24.8°C and rainfall of 534 mm.

The region's wetlands have been mapped and classified using a modified geomorphic wetland classification system (Semeniuk 1987) by the Department of Environment and Conservation (DEC) (2012a). This was a 'stage 2' mapping and classification exercise *sensu* Department of Environment and Conservation (2007), which means it was designed to provide 'preliminary evaluation and prioritisation for future detailed assessment'. The most extensive wetlands are seasonally inundated salt lakes, of which the northern examples are known as the Leeman Lagoons. Water depths in the playas are determined by direct rainfall, runoff, tidal fluctuations, evapotranspiration and groundwater discharge from the Tamala Limestone (Kern 1997,

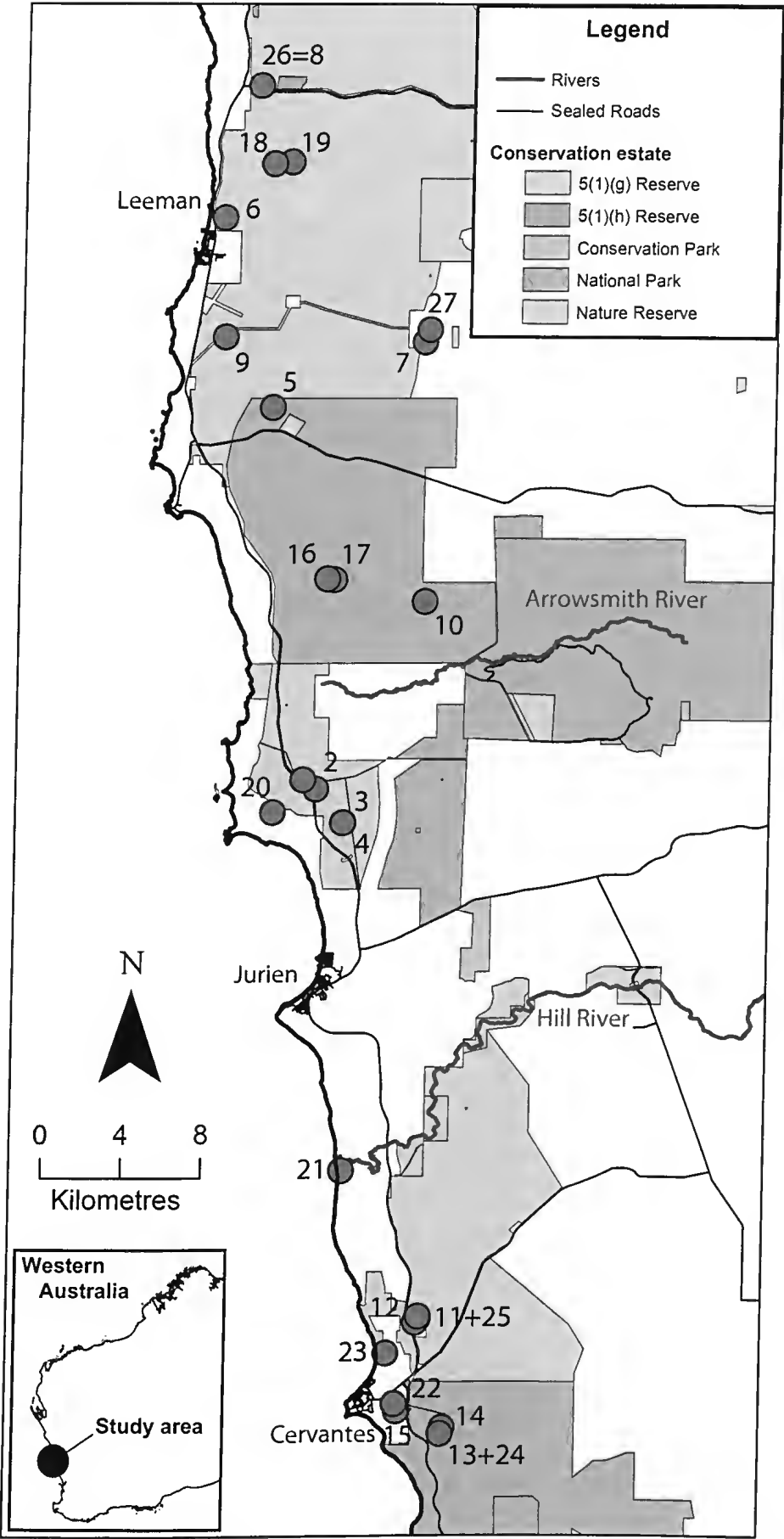


Figure 1. Map showing numbered sampling locations (see Table 1).

Table 1. List of wetlands sampled.

Site No.	Site name/location	Wetland type	Date sampled	Latitude (S)	Longitude (E)	Invertebrate community group	Geomorphic class
1	Salt lake 9km N of Jurien.	Seasonal saline playa	12/09/2011	30.207	115.038	1	Sumpland
2	Samphire flat S of site 1	Samphire flat	12/09/2011	30.202	115.031	3	Sumpland
3	Samphire flat adjacent to site 4	Samphire flat	13/09/2011	30.223	115.051	3	Sumpland
4	Sedge swamp adjacent to site 3	Sedge swamp	13/09/2011	30.223	115.051	3	Sumpland
5	Samphire flats N of Coorow-Greenhead Road	Samphire flat	13/09/2011	30.022	115.013	2	Barlkarra
6	Salt lake near Leeman = site sampled by Susac et al. (2009)	Seasonal saline playa	13/09/2011	29.929	114.989	1	Sumpland
7	Little Three Springs (southern occurrence)	Spring	14/09/2011	29.990	115.087	-	Spring
8-9/8-11	Salt lake north of Coolimba-Encabba Road = SPS178 of Pinder <i>et al.</i> (2004)	Seasonal saline playa	23/09/1999 14/09/2011	29.865	115.005	2	Sumpland
9	Salt lake 2km SSW of Leeman airstrip	Seasonal saline playa	14/09/2011	29.987	114.990	1	Sumpland
10	Diamond of the Desert Spring	Spring	15/09/2011	30.116	115.089	4	Spring
11	Samphire pan in Dingo Swamp complex	Samphire flat	16/09/2011	30.464	115.091	3	Sumpland
12	Salt lake in Dingo Swamp complex	Seasonal saline playa	16/09/2011	30.465	115.090	2	Sumpland
13	Claypan 4km ESE of Cervantes, Within wetland known locally as Bradley Springs	Seasonal freshwater lake	19/09/2011	30.518	115.103	5	Sumpland
14	Mound Spring 4km ESE of Cervantes. Within wetland known locally as Bradley Springs	Spring	19/09/2011	30.516	115.104	5	Spring
15	Lake Thetis	Permanent salt lake	19/09/2011	30.508	115.082	-	Lake
16	Eatha Spring	Spring	20/09/2011	30.105	115.045	-	Spring
17	Salt Lake adjacent to Eatha Spring	Seasonal saline playa	20/09/2011	30.105	115.041	1	Sumpland
18	Deadhorse Soak	Spring	21/09/2011	29.902	115.020	5	Palusplain
19	Sedge swamps west of Deadhorse Soak	Sedge fringed seasonal freshwater lake	21/09/2011	29.903	115.012	5	Sumpland
20	Moat wetland	Saline moat around earth mound	22/09/2011	30.218	115.017	2	Self-emergent
21	Sedge swamps at mouth of Hill River	Seepage fed sedge swamp	22/09/2011	30.392	115.053	3	Estuary-peripheral
22	Lake Thetis sedge swamp	Rehabilitated gravel pit	22/09/2011	30.505	115.080	5	Sumpland
23	Wealacutta Pool	Endorheic creekline	23/09/2011	30.480	115.076	5	River
24	Spring within site 13	Spring	27/02/2012	30.519	115.103	5	Spring
25	Spring in Dingo Swamp complex (within site 11)	Spring	27/02/2012	30.462	115.091	2	Sumpland
26	Little Three Springs (northern occurrence) = SPS202 of Pinder <i>et al.</i> (2004)	Spring	24/09/1999	29.865	115.005	4	Self-emergent

Rutherford *et al.* 2005). The salt lakes are fringed by complexes of samphire dominated flats and basins, sedge swamps and springs, many of which are connected during periods of high water levels. Many of the springs are also maintained by freshwater discharge from the Tamala limestone section of the superficial aquifer. Some of the springs lie next to, or even within, the saline wetlands. Further inland, the Eneabba aquifer and possibly the Lesueur aquifer discharge at a number of additional springs (e.g. Little Three Springs and Diamond of the Desert Springs) (Rutherford *et al.* 2005). The freshwater sedge swamp on the southern side of the Hill River estuary appears to be maintained by water seeping from the primary dunes. A discontinuous narrow channel between Cervantes and Jurien Bay wind through primary and secondary dunes and appear to be old creek lines that no longer have surface connections with the ocean but retain permanent water. A number of other more ephemeral wetlands in the primary dunes are present but were not sampled because they lacked surface water when visited and would rarely have much surface water at any time. Finally, Lake Thetis is a permanent, saline collapsed doline lake, again within the Tamala Limestone, with a rocky bed and stromatolites listed as a threatened ecological community (Grey *et al.* 1990, Department of Environment and Conservation 2012b). There are also a few streams traversing the plain, most of which discharge into wetlands and caves rather than to the sea, the exception being Hill River, but none of these were sampled.

METHODS

Site selection

Twenty five wetlands were selected to represent the range of wetland water chemistry, hydrology and morphology present within the study area (Fig. 1, Plate 1 and Table 1). Data from two sites sampled in 1999 by Pinder *et al.* (2004) were also included in our analyses. One of the latter is the same as site 8 sampled in 2011 for the present survey, so the two samples from this site are referred to as 8-99 and 8-11. The other site sampled in 1999 is referred to as site 26 in this paper but was coded as SPS202 by Pinder *et al.* (2004). Most wetlands are not formally named. Sampled wetlands included saline playas (sites 1, 6, 8, 9, 12 and 16, Plate 1F), samphire dominated flats or shallow basins (sites 2, 3, 5 and 11, Plate 1A), springs fed from groundwater discharging from the Tamala limestone and mostly within or adjacent to saline wetlands (sites 14, 16, 20, 24 and 25) (Plate 1E), more isolated eastern springs fed by the Eneabba and Lesueur aquifers (sites 7, 10 and 18, Plate 1B), a sedge swamp fed by water seeping from dunes at the mouth of the Hill River (site 21), a small area of sedges (site 4) watered by seepage from a dune near one of the salt lakes, a freshwater lake fringed by sedges (site 19, Plate 1D), Lake Thetis (site 15), an excavated wetland north of Lake Thetis (site 22) and Wealacutta Pool which is section of the relict stream channel north of Cervantes (site 23, Plate 1C).

Sampling

Water temperature and pH were measured in the field using a TPS WP-81 meter. Turbidity (nephelometric

turbidity units – NTU) was measured with a TPS WP-88 turbidity meter. Up to 900 mL of water was passed through a glass microfiber filter paper and the paper retained and frozen for analysis of chlorophyll concentration. The filtrate was passed through a 0.45 µm pore filter paper and frozen for analysis of total filterable nitrogen and phosphorus concentrations. Unfiltered water was collected for analysis of total phosphorus and nitrogen concentrations, colour (true colour units – TCU) and concentrations of major ions. Analytical methods were APHA *et al.* (2012) 4500N-C,I for total and filterable nitrogen and phosphorus, APHA *et al.* (2012) 4500NO3-I for nitrate+nitrite, APHA *et al.* (2012) 2540C for total dissolved solids, APHA *et al.* (2012) 2120-C for colour, APHA *et al.* (2012) 1020 for chlorophyll concentration, APHA *et al.* (2012) 3120 for K⁺, Na⁺, Ca²⁺ and SO₄²⁻, colourimetric analysis for Cl⁻ and APHA *et al.* (2012) 2320 for bicarbonate/carbonate/alkalinity. All analyses performed by ChemCentre (www.chemcentre.wa.gov.au) on samples submitted 1 to 3 weeks after collection.

At each site two invertebrate samples were collected: a plankton sample using a net with 50 µm mesh to sweep through the water column and gently through sparse vegetation and a benthic sample using a net with 250 µm mesh to sample the dominant habitats (e.g. open water, detritus, vegetation and substrates). Each sample involved sweeping for a total of about 50 m (usually not contiguous). The benthic samples were elutriated in the field to remove heavier inorganic material, leaves and woody debris were washed and discarded and then the sample was preserved in ethanol. The plankton sample was preserved in buffered formalin. The entire contents of each sample were sieved and sorted in the laboratory and representatives of each taxon seen during sorting were removed. Invertebrates, other than rotifers and protozoans, were identified to species level where possible.

Data analysis

All analyses were performed using either the R statistical software v 3.0.0 (R Development Core Team 2013) run within RStudio 0.97.449 (RStudio 2013) or with Primer (Primer-E Ltd 2008). The dissimilarity index for all multivariate analyses was Bray-Curtis. Agglomerative cluster analysis of the invertebrate data was performed using the function *hclust* (R Development Core Team 2013) using average linkage and significance of clusters was tested using *simprof* in package *clustsig* (Whitaker & Christman 2010). Non-hierarchical cluster analysis was performed using the *PAM* function (partitioning around medoids) in the cluster package v 1.14.4 (Maechler 2013). The *simper* routine in *vegan* (Oksanen *et al.* 2013) was used to identify species characteristic of community groups identified by the cluster analysis. Non-metric multidimensional scaling ordinations were performed using the *metaMDS* function in the *vegan* package. These analyses excluded taxa not identified to at least family level and identifications were sometimes merged or excluded where identifications were incomplete (e.g. where there were only juveniles or the wrong sex). Concentrations of major ions were converted to percent contribution to total millequivalence of anions or cations. Abiotic variables were transformed to approximate normality and where two variables were highly

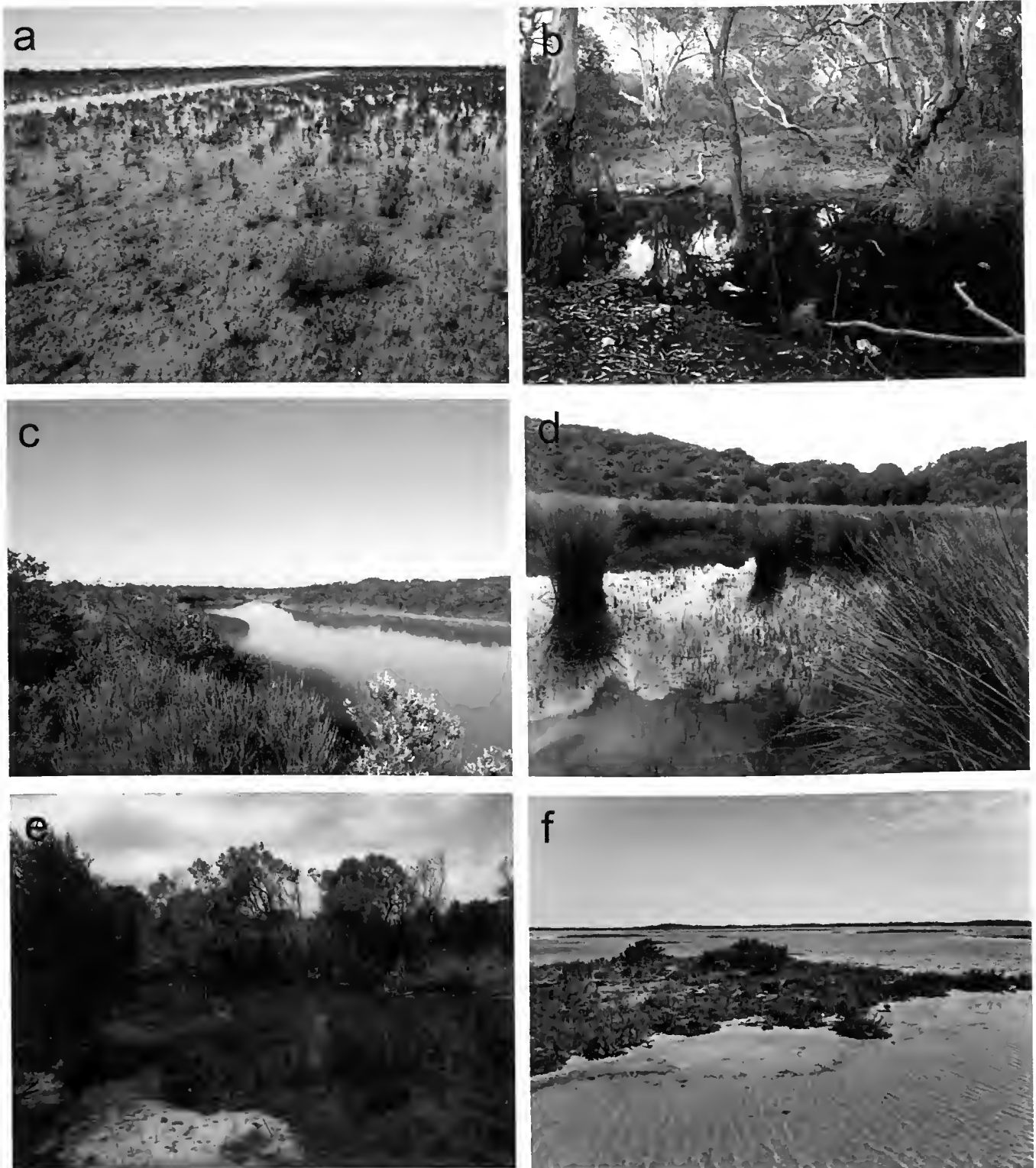


Plate 1. Photographs of representative wetlands. A, site 2: a samphire dominated flat; B, site 10, Diamond of the Desert Spring; C, site 23: Wealacutta Pool; D, site 19, a large freshwater sedge dominated wetland; E, site 14, pool on the edge of a mound spring ESE of Cervantes; F, site 9: a saline playa SSW of Leeman.

correlated ($r^2 > 0.9$) one was excluded from analyses. Distance-based redundancy analysis (db-RDA in the Primer DistLM routine) was used to identify variables that individually explained a significant proportion of

variation in community composition, and these were then used in a multi-variable db-RDA, using step-wise model building. R^2 adjusted for number of parameters was used to assess model performance.

RESULTS

Physico-chemical environment

Table 2 lists physical and chemical data for the 25 wetlands sampled in 2011/12 and the two sites sampled by Pinder *et al.* (2004). Most sites were shallower than 50 cm when sampled, with the deepest being Lake Thetis at 110 cm. Total dissolved solids ranged from 0.66 g/L (site 10, Diamond of the Desert Spring) to 97 g/L (site 8-11 salt lake north of Coolimba-Eneabba Road), with 7 sites being fresh (< 3 g/L), 8 subsaline (3 to <10 g/L) and 12 saline (≥ 10 g/L). All were Na^+ and Cl^- dominated, mostly with Na^+ >70% (of milliequivalence) and Cl^- > 80%. Site 14 (a

mound spring within the Bradley Springs complex) was notable for having only 59% Na^+ and 66% Cl^- , compensated for by higher Ca^{2+} and HCO_3^{2-} than all other sites. Based on ionic composition, salts in most of the saline wetlands (tds >10 mg/L) would precipitate via pathway 1A of Radke *et al.* (2002) (precipitation to Na^+ , Ca^{2+} , Mg^{2+} and Cl^-) except for 8-99 and site 5 (samphire flats north of Coorow-Greenhead Road) which would precipitate to Na^+ , Mg^{2+} , Cl^- and SO_4^{2-} via pathway 1B.

Clear water was the rule ($\text{NTU} \leq 33$), although site 25 (the spring in Dingo Swamp) had a higher than average turbidity of 94.8 NTU resulting from fine clays accumulating at the spring following water receding in

Table 2. Physical and chemical data for the sampled wetlands. The numbers for macrophyte cover and substrate are ranges of estimated surface area coverage: 1 = <20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = >80%.

	Site number (see Table 1)													
	1	2	3	4	5	6	7	8-11	8-99	9	10	11	12	13
Habitat														
Submerged macrophyte cover (%)	1	1	5	1	1	3	0	0	2	4	2	5	1	5
Emergent macrophyte cover (%)	0	3	2	5	5	0	0	0	2	1	1	1	3	1
Depth (cm)	15	12	28	21	70	26	35	10	70	10	34	45	14	110
Water chemistry														
Total dissolved solids (g/L)	28	12	6.8	6.6	34	71	4.8	97	24	55	0.66	8.5	27	5.4
Sum major ions (mg/L)	26.7	12.0	6.9	6.8	32.0	71.5	5.5	92.9	22.8	54.3	0.8	8.2	24.3	5.8
pH	8.68	8.92	8.47	7.88	8.07	8.34	7.90	8.31	8.62	8.68	7.81	8.59	8.98	9.02
Total nitrogen (mg/L)	1.2	5.6	3.3	3.4	4.2	1.3	2.2	4.6	–	3.3	0.46	2.6	3.7	1.7
Total filterable nitrogen (mg/L)	1.1	2.4	3.3	1.9	3.2	1.3	1	3.2	1.4	2.7	0.43	1.2	1.5	1.4
Nitrate (mg/L)	<0.01	<0.01	0.01	0.02	0.02	0.01	0.03	<0.01	0.01	0.01	0.01	0.01	0.01	0.03
Total phosphorus (mg/L)	<0.01	0.34	0.03	0.1	<0.01	<0.01	0.61	0.01	–	<0.01	0.02	0.01	0.02	<0.01
Total filterable phosphorus (mg/L)	<0.01	<0.01	0.02	0.05	<0.01	<0.01	0.33	<0.01	0.02	<0.01	<0.01	<0.01	<0.01	<0.01
Total chlorophyll (mg/L)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.009	<0.001	0.005	<0.001	<0.001	<0.001
Temperature (°C)	26.4	27.4	17.9	16	30.4	27.6	17.5	29.9	23.1	28.1	24.5	18.9	20.2	19.2
Turbidity (NTU)	1.2	11.5	1.6	1.6	3	0.8	19.4	5.5	2.6	11.8	10.5	0	3.6	0.5
Colour (TCU)	5	46	220	310	180	5	280	6	16	9	120	100	22	82
Sodium (% millequivalents)	77.03	79.73	77.35	76.14	74.99	83.88	73.78	81.21	72.17	78.34	82.93	76.60	77.51	80.59
Calcium (% millequivalents)	4.41	4.93	6.69	8.08	15.32	5.70	10.18	6.45	12.96	7.03	6.21	8.32	8.55	6.22
Magnesium (% millequivalents)	16.75	13.34	14.26	14.11	8.00	8.44	10.95	9.56	13.34	12.65	9.43	12.66	12.01	11.34
Potassium (% millequivalents)	1.81	2.00	1.70	1.67	1.69	1.98	5.09	2.78	1.52	1.97	1.43	2.42	1.93	1.85
Chloride (% millequivalents)	80.58	86.74	83.65	83.55	86.22	90.94	79.11	90.95	81.89	86.64	85.20	81.87	83.30	88.09
Sulphate (% millequivalents)	18.87	11.15	10.25	9.72	12.80	8.86	2.76	8.93	17.57	13.17	5.59	15.06	16.35	9.17
Bicarbonate (% millequivalents)	0.35	2.09	6.08	6.72	0.98	0.13	18.11	0.09	0.53	0.08	9.08	2.42	0.18	1.77
Carbonate (% millequivalents)	0.20	0.01	0.01	0.01	0.00	0.07	0.02	0.04	0.01	0.10	0.13	0.65	0.17	0.98
Substrate														
silt+clay	3	2	2	1	5	1	2	3	5	4	3	4	5	4
sand+gravel	3	4	5	5	1	5	4	3	0	2	3	2	2	3
pebble+cobble	0	0	0	0	0	0	0	0	0	0	1	0	0	0
boulder	0	0	0	0	0	0	0	0	0	0	0	0	0	0
bedrock	0	0	0	0	0	0	0	0	0	0	0	0	0	0
organic soil	0	0	0	0	0	0	0	0	–	0	0	0	0	0
benthic mats	1	1	5	0	5	1	0	5	–	4	0	4	0	0
particulate organic matter	0	1	0	2	0	0	5	0	1	0	5	0	0	1
litter (leaves and sticks)	0	1	0	2	1	0	4	0	1	1	5	0	0	1
logs	0	0	0	0	0	0	0	0	0	0	1	0	0	1

the samphire pan (site 11) in which the spring lies. No sites had particularly coloured water, although the hydrologically connected and groundwater-fed sites 3 and 4 had water with 220 and 310 TCU respectively and site 7 (southern occurrence of Little Three Springs) had 280 TCU, the latter probably a result of tannins from the abundant leaf litter.

About half of the sites had no detectable phosphorus and most of the rest had concentrations at or only slightly above detection limits (0.01 to 0.02 mg/L). The most notable exceptions for phosphorus being site 2 (one of the samphire flats) and site 7 (southern occurrence of Little Three Springs) which had 0.34 mg/L and 0.61 mg/L total phosphorus respectively. Site 2 had no detectable

filterable phosphorus which means it was all in particulate form or biologically assimilated. There was also no detectable chlorophyll at that site but there was an abundance of the cladoceran *Daphnia wardi* so the phosphorus may have been largely assimilated by grazing on phytoplankton. Site 7 also had no detectable chlorophyll even though half of the phosphorus was dissolved. This site consisted of a series of isolated shallow pools (the water sample was taken from the largest pool) with abundant leaf litter so the phosphorus may have come from decaying plant matter plus animal faeces around these, with algal growth limited by the dense canopy cover. Some sites had moderately high nitrogen (total > 3 mg/L) but these were all sites with TDS >6 g/L and some saline wetlands tend to be naturally

Table 2. (cont.)

	Site number (see Table 1)												
	14	15	16	17	18	19	20	21	22	23	24	25	26
Habitat													
Submerged macrophyte cover (%)	4	0	0	1	5	5	1	5	5	5	0	0	1
Emergent macrophyte cover (%)	1	1	5	1	1	3	1	5	5	1	1	1	1
Depth (cm)	41	120	15	20	37	15	36	50	25	45	77	23	40
Water chemistry													
Total dissolved solids (g/L)	0.76	50	16	66	2	2.3	27	3.3	3	5.7	1.3	0.98	2.3
Sum major ions (mg/L)	0.9	49.4	15.9	68.3	2.3	2.5	24.0	3.3	3.2	6.0	1.5	1.1	2.5
pH	7.99	8.14	7.17	7.90	7.60	7.54	7.83	7.02	8.05	9.18	8.25	7.95	8.1
Total nitrogen (mg/L)	2	3.1	2.3	1.9	0.54	0.37	4.6	1.6	1	2.8	2.6	0.54	–
Total filterable nitrogen (mg/L)	2	2.9	2.3	1.6	0.54	0.29	4	0.76	1	1.8	2.6	0.54	0.77
Nitrate (mg/L)	1.7	0.01	1.8	<0.01	0.24	0.17	0.02	<0.01	<0.01	0.01	11	0.31	<0.02
Total phosphorus (mg/L)	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	0.07	0.01	0.01	<0.01	<0.01	–
Total filterable phosphorus (mg/L)	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01
Total chlorophyll (mg/L)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.001	<0.001	<0.001	0.002	0.001	0.01
Temperature (0C)	23.2	20.6	21.8	25	21.2	21.2	–	19.5	20	13	23.8	29.3	18
Turbidity (NTU)	0	0	0	11.5	1	0	0.4	2.8	1.8	33	8.1	94.8	4.5
Colour (TCU)	6	2	3	4	26	11	190	190	100	27	6	10	100
Sodium (% millequivalents)	59.24	83.02	80.97	80.83	73.92	71.11	76.62	81.25	75.61	80.92	62.61	59.79	77.78
Calcium (% millequivalents)	30.55	3.26	6.46	6.72	16.61	19.40	9.00	5.54	9.86	1.52	22.10	23.16	4.89
Magnesium (% millequivalents)	8.81	11.32	10.93	10.01	7.66	8.08	12.40	11.20	12.70	15.63	14.12	15.08	14.29
Potassium (% millequivalents)	1.41	2.41	1.63	2.44	1.81	1.41	1.98	2.01	1.82	1.93	1.17	1.97	3.04
Chloride (% millequivalents)	66.41	91.57	89.67	89.25	82.08	80.27	86.41	87.73	80.45	85.48	72.37	68.65	81.72
Sulphate (% millequivalents)	5.47	7.79	8.44	10.55	4.13	5.19	11.54	7.72	8.42	6.22	6.96	7.56	3.47
Bicarbonate (% millequivalents)	28.00	0.50	1.88	0.19	13.74	14.50	2.04	4.52	11.10	4.83	20.52	23.61	14.73
Carbonate (% millequivalents)	0.11	0.14	0.01	0.02	0.05	0.04	0.00	0.03	0.03	3.47	0.14	0.18	0.08
Substrate													
silt+clay	3	0	3	3	1	4	5	4	2	1	5	5	1
sand+gravel	2	1	1	3	1	2	1	3	5	5	1	1	5
pebble+cobble	0	1	0	0	1	0	0	0	0	0	0	0	1
boulder	0	1	0	0	0	0	0	0	0	0	0	0	0
bedrock	0	4	0	0	4	0	0	0	0	0	0	0	0
organic soil	1	0	3	0	0	0	0	0	0	0	0	0	–
benthic mats	0	0	0	0	0	0	5	1	0	0	0	0	–
particulate organic matter	0	0	0	0	0	0	1	0	0	5	0	0	–
litter (leafs and sticks)	1	0	1	0	1	1	1	1	1	1	0	0	2
logs	0	0	1	0	0	0	0	0	0	0	1	0	1

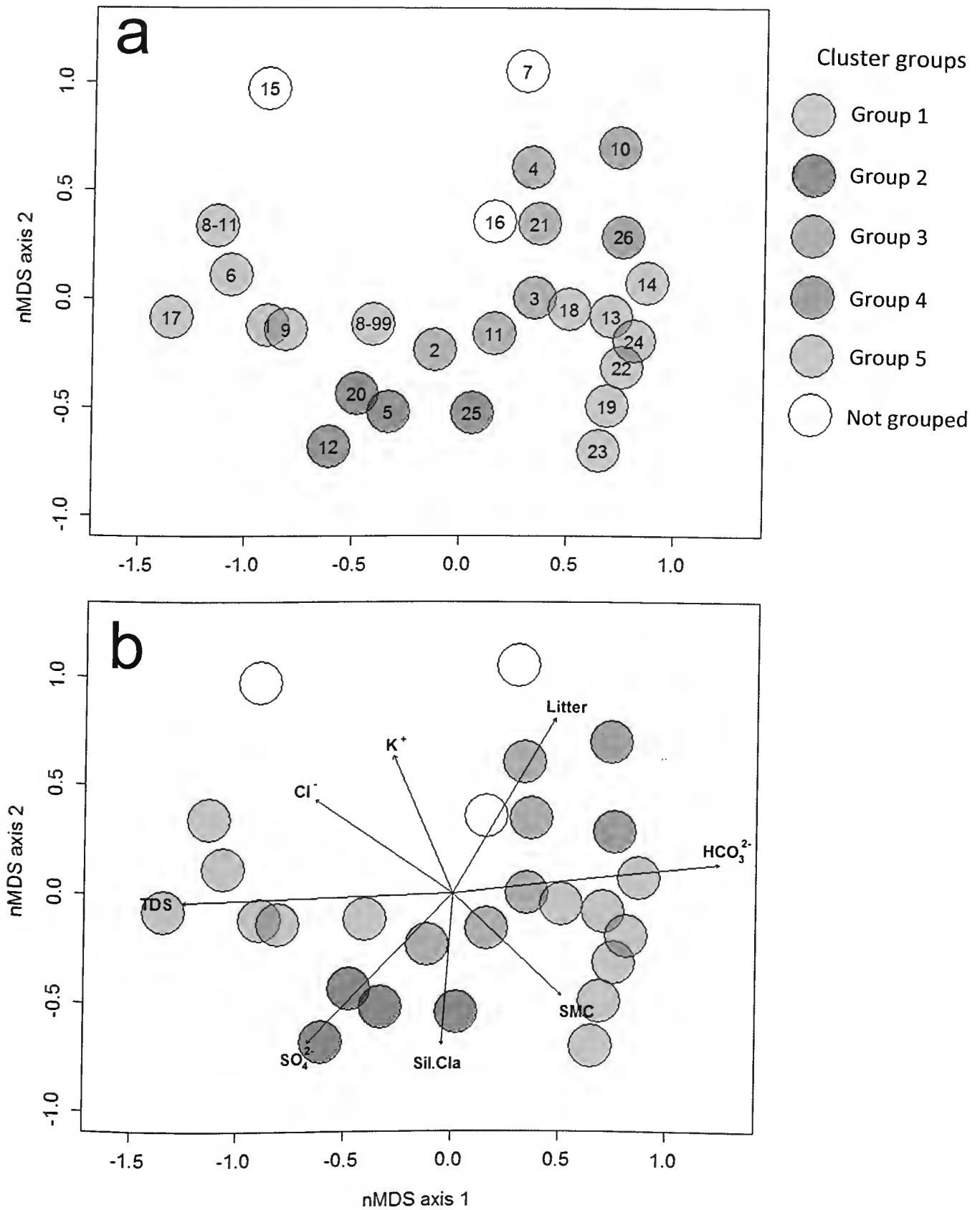


Figure 2. Two dimensional nMDS ordination of the Jurien invertebrate data. a, plot showing numbered sites coloured according to their membership of groups in the cluster analysis; b, same ordination with vectors indicating direction and strength of the relationships between environmental variables and ordination axis scores (representing community composition). TDS = total dissolved solids, Litter = leaf litter cover class, Logs = log cover class, SMC = submerged macrophyte cover class, Sil.Cla = silt+clay cover class. Stress = 0.17.

high in nitrogen (Pinder *et al.* 2004). Average nitrogen concentration in freshwater wetlands was 1.1 g/L. Only two sites had chlorophyll much above the limit of detection (0.001 mg/L): site 27 (northern Little Three Springs) with 0.01 mg/L and site 26 (the playa north-east of Jurien Bay) with 0.009 mg/L.

Sediments were mostly dominated by silt/clay or sand/gravel or both, but Lake Thetis (site 15) and Deadhorse Soak (site 18) had limestone beds while site 16 (Eatha Spring) had primarily organic substrate. Few other sites had much organic matter, but the southern Little Three Springs (site 7) and Diamond of the Desert Spring (site 10) both had a layer of litter and particulate organic matter over the sediment and the palaeocreek (site 23) had a layer of organic particulates over the bed. Some of the samphire flats and other saline sites (sites 3, 5, 9 and 20) had mats of benthic algae. Coarse organic debris was usually scattered, except at site 7 (southern Little Three Springs) and site 10 (Diamond of the Desert Spring) which both consisted of pools under a canopy of trees.

Most of the saline playas had partial to nearly complete cover of *Ruppia* and/or Characeae across the bed though some were largely bare. These were invariably fringed by *Tecticornia* dominated plant communities, with this sometimes inundated. The *Tecticornia* dominated saline flats also often had a cover of *Ruppia* and/or Characeae, sometimes with patches of sedges. The palaeocreek had an almost complete and dense cover of Characeae with a narrow fringe of sedges along the banks. The springs varied from having no submerged or inundated plants (e.g. southern Little Three Springs, site 7) to almost complete cover of emergent macrophytes (Eatha Spring, site 16) or submerged macrophytes (Deadhorse Soak, site 18).

Invertebrate diversity

A total of 195 aquatic invertebrate taxa were collected during the survey reported here and an additional 20 species were recorded in the two sites sampled by Pinder *et al.* (2004), bringing the total to 215 taxa (Appendix 1). One of the species collected in 2011 (a *Lynceus* clam shrimp) was an opportunistic collection from a drying freshwater flat and was not included in analyses. Richness per sample ranged from 8 (site 6: one of the saline playas) to 72 (site 26: northern Little Three Springs) with an average of 30 and a median of 28. Most species collected in the present study (119) were insects, of which 36 were beetles and 48 were diptera. Most non-insects were ostracods or copepods (22 and 23 species respectively), annelids (12), water mites (12) or cladocerans (10). The frequency distribution of species occurrence was highly skewed with 43% of species occurring only once and only 8% occurring in more than a third of sites. Just over 40% of those singleton species occurred in one of just three wetlands: Deadhorse Soak (site 18), the sedge swamps west of Deadhorse Soak (site 19) and northern Little Three Springs (site 26).

Invertebrate community classification

The agglomerative cluster analysis of sites based on their invertebrate communities produced a dendrogram with five cluster groups, all supported by a simprof analysis,

Table 3. Summary statistics for the invertebrate community groupings from the cluster analysis.

Group	Number of sites	Number of species in group	Number of species unique to group/site	Average richness	Salinity range (g/L)
1	6	38	4	14	24–71
2	4	52	5	21	(0.98) 27–34
3	5	89	18	38	3.3–12
4	2	79	26	50	0.66–2.3
5	7	127	60	42	0.76–5.7
site 7		20	5	–	4.8
site 15		10	5	–	50
site 16		27	4	–	16

plus three sites that did not group with any others, at a uniform dissimilarity value of 0.30. PAM cluster analyses with 3 to 8 groups produced almost identical clustering, including separation of the same three individual sites at the 8 group level, so the hierarchical nature of the agglomerative analysis did not constrain optimisation of clustering. These groups also largely separated from one another in a two-dimensional ordination (Fig. 2a). Summary statistics for these communities are provided in Table 3 which shows that 127 species (about 60% of the total) only occurred in one of the cluster groups or in one of the three sites that didn't group with others. The highest level grouping in the cluster analysis separated the more saline wetlands (groups 1 and 2 plus Lake Thetis: tds 0.98 – 97 g/L, median 31) from fresh to subsaline wetlands (groups 3 to 5 plus Eatha Spring and northern Little Three Springs: TDS 0.66 – 16 g/L, median 4.8).

Group 1. Six saline seasonally inundated playas (24 to 97 g/L) that were fringed with samphire but with little to no samphire across the bed, and mostly with substantial cover of submerged macrophytes (mostly *Ruppia*). Communities in these wetlands were more likely than those of other wetlands to include a number of halophilic ostracods (*Diacypris compacta*, *Reticypris clava*, *Platycypris baueri* and *Australocypris insularis*) and the dipterans Dolichopodidae sp. and *Tanytarsus barbitarsus*.

Lake Thetis (site 15). The community from this permanent saline wetland included numerous species not found within the other surveyed wetlands, including *Capitella* polychaetes, the amphipod *Melita kauerti* and copepods Laophontidae sp. 1 and *Halicyclops spinifera*.

Group 2. Four moderately saline wetlands (0.98 to 34 g/L), including an open playa with *Ruppia*, two wetlands with extensive samphire communities on the bed and a freshwater spring. These wetlands tended to have finer sediments than those in group 1. The spring, site 25, was located in the middle of a samphire pan (site 11) and is only fresh once the pan dries. The fauna in this spring has to cope with the saline phase when the pan is flooded (tds of 8.5 when sampled but probably higher at times) so it is comprised of salt-tolerant species even when the fresh spring is the only water present. Compared to communities in other wetlands, group 2 had more frequent occurrence of the ostracod *Diacypris spinosa*, dipterans Stratiomyidae and Ephydriidae sp. JCS2, *Coxiella* snails, the beetle *Berosus discolor* and copepod *Apocyclops dengizicus*.

Eatha Spring (site 16). Despite its relatively high salinity of 16 g/L, this site clustered with fresh to subsaline swamps, probably because it consists of a freshwater seepage flowing into a salt lake. This is reflected in the invertebrate fauna including both halophilic species such as the midge *Tanytarsus barbitarsus* and cladoceran *Daphnia truncata*, euryhaline species such as the *Austrochiltonia subtennis*, and species more usually associated with freshwater. The dual nature of this site would have contributed to it clustering separately to other sites. It was also the only site with oribatid mite sp. JCS1, darwinulid ostracods and gilgies (*Cherax quinquecarinatus*).

Group 3. Communities inhabiting five subsaline to mildly saline wetlands (3.3 – 12 g/L) including three samphire flats and three sedge swamps, mostly with >50% emergent vegetation and some with extensive growth of submerged macrophytes. These wetlands tended to have higher nitrogen concentrations than other fresh to subsaline wetlands. These communities were characterized by more frequent occurrence of many species, most notably the ostracod *Cyprinotus cingalensis*, haliplid and scirtid beetles, mesostigmatid mites, chironomids *Tanytarsus semibarbitarsus* and *Corynoneura* sp. V49 and the copepod *Boeckella triarticulata*.

Group 4. Communities from two of the three more isolated inland springs: Diamond of the Desert Spring (site 10) and northern Little Three Springs (site 26). The other inland spring (the southern occurrence of Little Three Springs) clustered away from all other sites. These springs were both fresh and had little macrophyte growth, probably due to the canopy cover of the woodland in which they were situated which also contributed to relatively high amounts of decomposing leaf litter. A third of species occurring in one or both of these two wetlands did not occur in any other sites. These were the only communities with *Necterosoma darwini* and two of only three communities with the mosquito *Aedes alboannulatus* and non-biting midge *Forcypomia* sp.

Group 5. Communities from seven fresh to subsaline wetlands (0.76 to 5.7 g/L), including most of the remaining springs, sedge swamps, seasonal lakes and Wealacutta Pool (site 23). Many of these wetlands had relatively high $\%Ca^{2+}$ and $\%HCO_3^{-} + CO_3^{2-}$, reflecting their association with groundwater discharge from the Tamala limestone, and all but one had $\geq 60\%$ submerged macrophyte cover. Nearly half of the species collected from these wetlands were not found in wetlands of other cluster groups. These communities were distinguished from those in other groups by more frequent occurrence of the chironomids *Tanytarsus fuscithorax* and *Polypedilum nubifer*, the hemipteran *Anisops thienemanni* and copepod *Mesocyclops brooksi*.

Southern Little Three Springs. This community inhabited small, shallow, litter-filled pools on a woodland floor. It was the only community to have the oligochaete *Ainudrilus nharna*, pezid mites, the beetle *Enochrus maculiceps* and the crane fly Tipulidae type C.

Invertebrate – environment relationships

Grouping of the sites in the cluster analyses suggested that communities varied along salinity and vegetation gradients. Total dissolved solids and % submerged

macrophytes were amongst the eight environmental variables correlated with axis scores of the nMDS ordination (p-value < 0.05, r^2 0.24 to 0.82): the others being % cover of litter, $\%Cl^{-}$, $\%HCO_3^{-}$, $\%SO_4^{2-}$ and $\%K^{+}$ and cover of silt+clay. These variables are shown as vectors reflecting the strength and direction of their correlations with the nMDS axes on Fig. 2b. These vectors show composition aligned along a salinity gradient, with saline sites to the left and the freshest sites to the right. The relationship between salinity and the biota is not entirely aligned with vectors for the relative concentrations of ions. The most saline sites (≥ 60 g/L) to the left and top left of the nMDS plot tended to have highest $\%Cl^{-}$ (>88%) but so did Lake Thetis (site 15, tds 50 g/L) and even the salt lake influenced Eatha Spring (site 16, tds 16 g/L), while some of the more moderate saline lakes in the bottom left to centre of the plot had highest $\%SO_4^{2-}$. Some of the fresher sites had particularly high $\%HCO_3^{-}$ (> 10%), probably as a result of groundwater discharge from the Tamala limestone, but the more inland springs fed by discharge from the Lesueur Sandstone (sites 7, 10 and 26) and the lower salinity wetlands closer to the coast (such as sites 21 and 23), which may have a marine influence, did not. At the fresher end of the salinity gradient there was a separation of those wetlands with higher cover of litter (heavily shaded sites such as the Little Three Springs sites towards the top right of the plot) from wetlands with the most submerged macrophytes (which were more open wetlands). Wetlands with finer sediments tended to occur more towards the bottom of the ordination plot and included a salt lake, samphire flats and fresh springs in the middle of subsaline wetlands (where water levels receding to the springs may have led to accumulation of fine sediment).

Twelve environmental variables had significant individual correlations with invertebrate community composition in an initial db-RDA. Of these, $\%HCO_3^{-}$ and total dissolved solids were strongly correlated ($r^2 = 0.92$). Further analyses excluded total dissolved solids because it had a slightly lower individual correlation with community composition than $\%HCO_3^{-}$. A step-wise approach to variable selection using the remaining 11 variables produced a model with 9 variables explaining 60% of variation in composition, but four of these variables (cover of logs, depth, temperature and longitude) did not contribute significantly to the model. A final model with $\%HCO_3^{-}$, $\%Cl^{-}$, colour, submerged macrophyte cover and litter, all with significant partial contributions, explained 46% of variation in community composition.

These analyses indicate that wetland position and geomorphology, through influences on water chemistry, hydrology, vegetation structure, organic inputs and sediment composition, are important in structuring invertebrate communities of the region's wetlands.

DISCUSSION

Invertebrate diversity and distributions

Species richness is about what would be expected considering the nature of the wetlands: predominantly saline wetlands or small springs with low habitat

diversity. The average of 30 species per sample is lower than the average of 36 per sample recorded in 200 wetlands across the south-west agricultural zone sampled by Pinder *et al.* (2004) and the 39 per sample recorded in the Hutt catchments by Pinder *et al.* (2012). Fewer species (an average of 19 per sample) were recorded within the mostly saline Buntine Marchagee wetlands in the northern Wheatbelt sampled by Aquatic Research Laboratory (2004, 2006, 2009). All of these studies have used the same sampling and laboratory methods and all these figures exclude rotifers and protozoans, as in the present study.

Horwitz *et al.* (2009) suggest that local and regional endemism amongst Swan Coastal Plain aquatic invertebrates was relatively low compared to other regional assessments in WA. Our results suggest that this holds for the Jurien area which is near the plain's northern extent. However, while most of the invertebrates are common and widely distributed in south-western Australia or more widely, there are some exceptions. Although the leech *Goddardobdella elegans* is widely distributed in Australia there are few records of leeches from the mid-west of Western Australia (data from the Western Australian Museum and the Department of Parks and Wildlife), reflecting the generally saline and/or temporary nature of most of the region's wetlands, so its occurrence in the swamp north of Lake Thetis (site 22) is notable. However, subsequent

collecting in 2014 resulted in new (but unidentified) leech records from three other wetlands in the area (Dept Parks and Wildlife, unpublished data). The polychaete *Manayunkia* n. sp. is widely distributed in naturally saline lakes of the south-west (Pinder *et al.* 2004) but the record from site 12 is the first north of about Dowerin. The *Recifella* water mite from Wealacutta-Pool (site 23) has not been recorded in other Department of Parks and Wildlife invertebrate projects and may be new. Another mite, *Arrenurus* (*Truncaturus*) sp. 25, recorded from Deadhorse Soak (site 18) is otherwise known only from springs near the town of Three Springs (Pinder & Leung 2010) plus the groundwater fed Utcha Swamp near Hutt Lagoon (Pinder *et al.* 2012). The brine shrimp *Parartemia extracta* (from three of the saline playas) is known only from the central and northern Wheatbelt and these new records represent half of the known extant populations. Timms *et al.* (2009) suggest that this species is becoming less abundant in the northern Wheatbelt due to salinisation, with half of previously known populations possibly extinct and that it may be a threatened species. The relatively well protected playas along the Jurien coast may be an important refuge for this species and its distribution in the lakes should be further investigated. The harpacticoid copepod in the genus *Leptocaris* is similar to *Leptocaris brevicornis* (a widely distributed marine interstitial species also known from Fortescue Marsh in the Pilbara) but differs in sufficient detail to

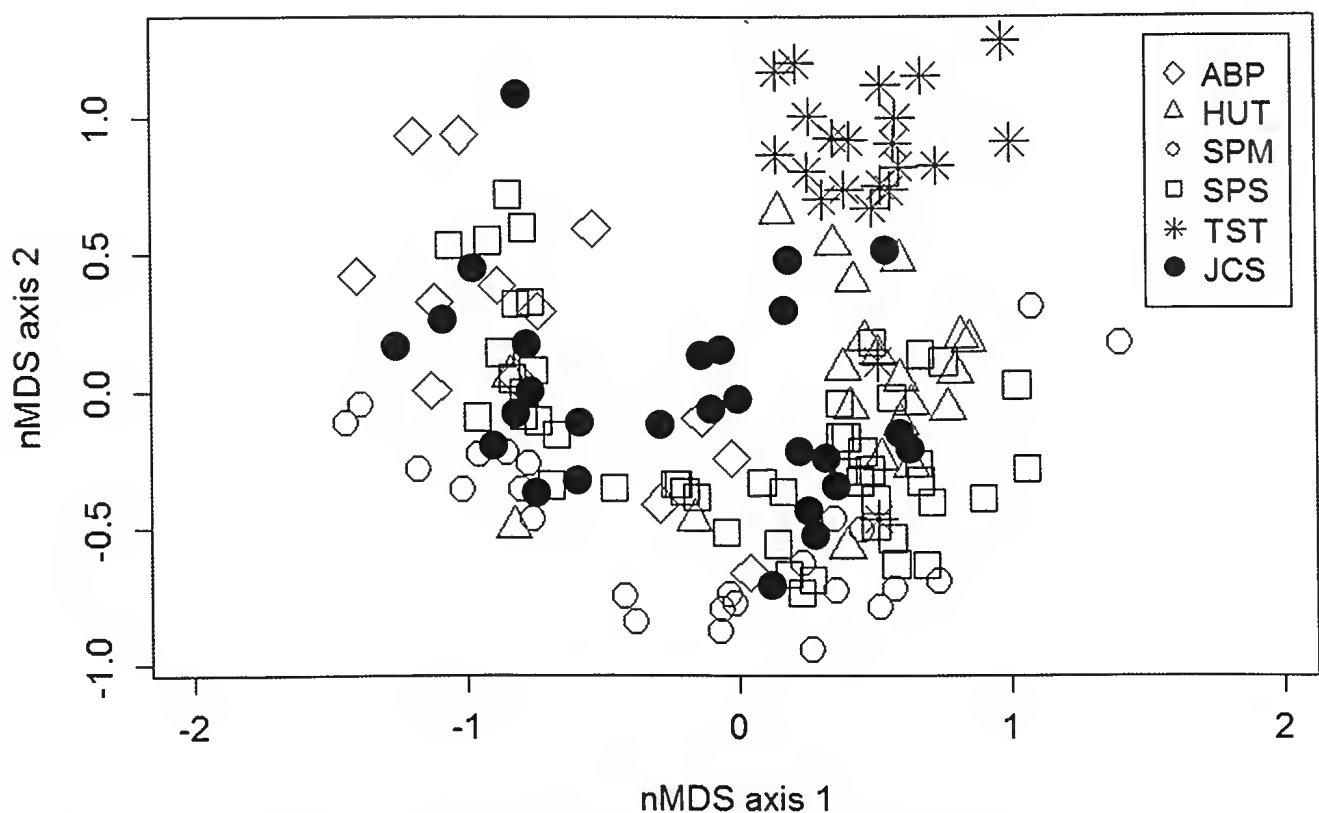


Figure 3. Axes 1 and 2 of a three dimensional ordination of aquatic invertebrate composition data from the present survey (JCS), northern Wheatbelt data from Pinder *et al.* (2004) (SPS), State Salinity Strategy wetland monitoring in the northern Wheatbelt by Cale *et al.* (2004 and unpublished data) (SPM), sites in the Hutt River/Hutt Lagoon catchments sampled by Pinder *et al.* (2012) (HUT), mound springs near the town of Three Springs at the headwaters of the Hill River sampled by Pinder and Leung (2010) (TST) and wetlands sampled in the northern Wheatbelt by Jones *et al.* (2009) (ABP). Stress = 0.15.

suggest that it may be a new species. It also differs from another new *Leptocaris* from Shark Bay (Jane McRae, Bennelongia Pty Ltd, pers. comm., 2 May 2012). A few other species have rarely been recorded in the mid-west and Wheatbelt, such as the water strider *Hydrometra strigosa* and *Hydrophilus* beetles. The occurrence of gilgies (*Cherax quinquecarinatus*) at Eatha Spring is the most northerly record known for this species (Pierre Horwitz, Edith Cowan University, pers. comm.).

Unlike the Hutt catchments, 200km further north, the Jurien fauna did not include a north-western element, although Pinder *et al.* (2004) collected a couple of such species from Lake Logue and Arro Lake just to the north-east of our study area. This fits with the notion that the northern element in the Western Australian aquatic invertebrate declines between the Murchison River and Eneabba (Pinder *et al.* 2004, 2012), excepting that a few such species do occasionally occur further south.

The composition of invertebrate communities in the Jurien wetlands is not distinct at a regional (northern Wheatbelt/southern Mid-west) scale. A three-dimensional ordination using data from other studies in the region with consistent taxonomy (Fig. 3) shows that there is considerable overlap in composition between Jurien communities and those in wetlands further inland and north. Axes 1 and 2 of the ordination are shown in Fig. 3 but other axis combinations did not show any greater separation of Jurien wetlands from others. This contrasts with the springs on the upper Hill River south of the town of Three Springs (TST sites in Fig. 3) which clearly support a distinctive assemblage of species, contributing to their status as threatened ecological communities. Jurien sites that were most separated in ordination space from other wetlands were Lake Thetis (top most Jurien site in Fig. 3) and three seepage fed vegetated swamps in the centre of the ordination (Eatha Spring, the sedge swamp near the mouth of Hill River and the seepage fed sedge swamp north of Jurien: sites 16, 21 and 4 respectively). Lake Thetis is a unique wetland type and freshwater sedge/rush dominated wetlands are rare in the broader region.

Geomorphic versus invertebrate classification

Table 1 lists the allocation of sites to the cluster groups based on invertebrate community composition and the geomorphic wetland class that they were assigned to by DEC (2012a). Seven of the 14 geomorphic wetland categories were represented in the sites reported here. Of these, only three were represented by more than one wetland: sumplands, springs and self-emergent wetlands. The latter were the saline moat wetland (site 20) and one of the freshwater Little Three Springs sites (site 26) but in the invertebrate analysis these sites clustered separately to one another within groups 2 and 4 respectively, reflecting differences in salinity. Fourteen sites were classified as sumpland (seasonally inundated basins) under the geomorphic system but these were spread over four of the invertebrate community groups. Most of these were salt lakes or samphire-dominated flats but there were also some freshwater swamps and springs. For the wetland mapping process, the two springs were evidently not sufficiently conspicuous (on aerial photographs and from other GIS data sources) to be distinguished from the larger wetlands within which

they sit, so the issue was one of resolution rather than classification. These were Deadhorse Soak (site 18) within a large palusplain and the spring in the Dingo Swamp complex (site 11) within a small samphire filled sumpland. That site 5 was classified as a balkarra (intermittently inundated flat) by DEC (2012a) may also have been a resolution issue as the sampled site was a small area (<1 ha) of inundated samphire set within a larger non-flooded area, so was probably a sumpland lying within a balkarra. Our sites that were classed as springs in the geomorphic classification were certainly all areas of groundwater discharge but they were spread over invertebrate community groups 4 and 5 plus two of the sites that did not cluster with other sites (sites 7 and 16). The 'estuary-peripheral' site (site 21) was certainly on the edge of the Hill River mouth, but its invertebrate community grouped with other fresh to sub-saline vegetated swamps in group 5. Lake Thetis did not cluster with other wetlands in the invertebrate analysis and was the only site classed as a 'lake' by DEC (2012). Finally, Wealacutta Pool (site 23) was classed as a river in the geomorphic system but it grouped with other fresh to subsaline wetlands with emergent vegetation in invertebrate community group 5 above, reflecting its contemporary lentic nature. There was clearly little alignment between the cluster groups derived from the invertebrate community composition and the classification of the same sites based on the geomorphic system. Our analyses suggest that if the structure and cover of aquatic and fringing vegetation and some indication of salinity range were included in the classification system, as proposed in a newer expanded geomorphic system (Semeniuk & Semeniuk 2011), and as used in some other wetland classification systems (e.g. Duguid *et al.* 2005), then a better alignment with invertebrate biodiversity might be achieved.

Groundwater dependence

One of the aims of this study was to assess the degree to which the epigeal aquatic invertebrate fauna is dependent on groundwater. The only invertebrates collected in this study that are known to be stygophilic are the unidentified darwinulid ostracods from Eatha Spring (site 16) which may be widespread in the underlying superficial aquifer. By comparison, springs in the upper Hill River north-east of the study area have darwinulid ostracods plus stygal candonid ostracods, bathynellids and phreodrilid oligochaetes which may also inhabit the associated groundwater (Pinder and Leung 2010). Nor was there a suite of epigeal species known to be closely associated with spring habitats elsewhere, as is also the case in the Hill River springs. An exception might be the water mite *Arrenurus* sp. 25 from Deadhorse Soak, which is otherwise known only from the Hill River springs (Pinder and Leung 2010) and the groundwater-fed Utcha Swamp north of Hutt Lagoon (Pinder *et al.* 2012). Also unlike the Hill River springs and the springs in the Hutt River Catchments, the Jurien springs do not support south-west mesic-adapted species that are otherwise rare north of Perth, such as the dragonfly *Archaeosynthemis occidentalis* and trichopteran *Notoperata tenax*. Nonetheless, with at least some of the springs being permanent and fresh, they are likely to be acting as local drought refuges for many of the species collected in the study area. Some active dispersers such

as the dragonfly *Orthetrum caledonicum*, beetle *Allodessus bistrigatus*, backswimmer *Anisops theinmanni* and chironomid *Tanytarsus fuscithorax* were present in most of the springs and probably disperse from these to the less permanent wetlands following dry periods. These and other species, such as many of the water mites, may also occur preferentially in the springs because of the reliably fresh water whereas many other wetlands are saline much of the time. Despite their lack of a characteristic spring associated fauna, these sites are likely to be critical for maintaining the regional diversity of aquatic invertebrates, with the eight springs collectively supporting 147 species, which is nearly as many as the other 19 sites combined (154).

Salt lake faunas

The other main driver of this survey was the need to understand the diversity and distribution of invertebrates in the saline playas that may be subject to expansion of gypsum mining in the future. These playas (sites 1,6,8,9,12,17 and 26) supported a total of 45 species, with 8 to 21 species per wetland. Several of those taxa could not be resolved to species level so their conservation status couldn't be assessed (e.g. *Coxiella* snails and mesostigmatid mites). Most of the rest are halophilic species, such as the copepod *Apocyclops dengizicus* and beetle *Necterosoma penicillatus*, that are very widespread in south-western Australia (and beyond for some species). Two species were of note: the polychaete *Manayunkia* n. sp. and the brine shrimp *Parartemia extracta*, both discussed above. Previous records of *Manayunkia* have been from wetlands with salinities ranging from 17 to 120 g/L (Pinder *et al.* 2004 and Department of Parks and Wildlife unpublished data), but with a median salinity of 46 g/L. In the Jurien area it was collected from site 12 (27 g/L) whereas four of the remaining salt lakes (lacking *Manayunkia*) had salinity >54 g/L. *Parartemia extracta* was also recorded only at the lower end of the salinity range of these wetlands (27 to 55 g/L) which is within the previously known salinity occurrence range of the species: 27 to 100 g/L (Timms *et al.* 2009). That no more than half of the salt lake fauna occurred in any one of the playas indicates that these wetlands have heterogeneous faunas and that preservation of multiple representatives is required to ensure the persistence of the full salt lake fauna of the region.

SUMMARY

Wetlands are a prominent feature of the Jurien coastal landscape and one of only a few such wetland complexes along the western coast of Australia. This study has surveyed the dominant faunal group inhabiting these wetlands, finding that the region has about average diversity for the types of wetlands present and compositions not dissimilar to those of wetlands elsewhere in the northern Wheatbelt and mid-west coast. Most species were common and widespread, but some rare and/or restricted species were present. While there were very few species closely associated with groundwater or with springs, the springs are undoubtedly important in maintaining aquatic invertebrate diversity in the study area by providing a

freshwater drought refuge for much of the fauna. The salt lakes may be particularly important for the brine shrimp *Parartemia extracta*, but further survey for this species in the region and in the broader northern Wheatbelt is required to determine its conservation status.

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REFERENCES

- AMERICAN PUBLIC HEALTH ASSOCIATION, AMERICAN WATER WORKS ASSOCIATION & WATER ENVIRONMENT FEDERATION 2012. Standard Methods for the Examination of Water and Wastewater. In: Rice E W, Baird R B, Eaton A D and Clesceri L S (eds). American Public Health Association, Washington, D.C.
- AQUATIC RESEARCH LABORATORY 2004. Buntine-Marchagee Natural Diversity Recovery Catchment (BMRC). Wetland Invertebrate Fauna Monitoring: August 2004. Report to the Department of Conservation and Land Management. Aquatic Research Laboratory, University of Western Australia, Perth.
- AQUATIC RESEARCH LABORATORY 2006. Buntine-Marchagee Natural Diversity Recovery Catchment (BMRC). Wetland Invertebrate Fauna Monitoring: August 2005. Report to the Department of Conservation and Land Management. Aquatic Research Laboratory, University of Western Australia, Perth.
- AQUATIC RESEARCH LABORATORY 2009. Buntine Marchagee Natural Diversity Recovery Catchment (BMNDRC). Wetland Invertebrate Fauna Sampling: 2008. University of Western Australia, Perth.
- BIOTA ENVIRONMENTAL SCIENCES 2002. Jurien Ecological Water Requirements Subterranean Fauna Study. Undertaken for Welker Environmental Consultancy and Water Corporation. Biota Environmental Sciences, Perth.
- CALE D J, HALSE S A & WALKER C W 2004. Wetlands monitoring in the Wheatbelt of south-west Western Australia: site descriptions, waterbird, aquatic invertebrate and groundwater data. *Conservation Science Western Australia* 5, 20–135.
- COMMONWEALTH OF AUSTRALIA 2012. Interim Biogeographic Regionalisation for Australia, Version 7.
- CONSERVATION COMMISSION OF WESTERN AUSTRALIA, DEPARTMENT OF ENVIRONMENT AND CONSERVATION & CITY OF ROCKINGHAM 2010. Rockingham Lakes Regional Park. Management Plan No. 67.

- DEPARTMENT OF ENVIRONMENT AND CONSERVATION 2007. Framework for mapping, classification and evaluation of wetlands in Western Australia. Department of Environment and Conservation, Perth.
- DEPARTMENT OF ENVIRONMENT AND CONSERVATION 2012a. Western Australian wetland inventory series. Wetland identification, delineation and classification: methodology and results for the geomorphic wetlands Cervantes Coolimba coastal stage 2 dataset. Department of Environment and Conservation, Perth.
- DEPARTMENT OF ENVIRONMENT AND CONSERVATION 2012b. Interim Recovery Plan 2012–2017 for the Stromatolite community of stratified hypersaline coastal lake – Lake Thetis. Interim Recovery Plan No. 325. Department of Environment and Conservation, Perth.
- DUGUID A, BARNETSON J, CLIFFORD B, PAVEY C, ALBRECHT D, RISLER J & McNELLIE M 2005. Wetlands in the Arid Northern Territory. A report to the Australian Government Department of the Environment and Heritage on the inventory and significance of wetlands in the arid NT. Northern Territory Government Department of Natural Resources, Environment and the Arts, Alice Springs.
- GOVERNMENT OF WESTERN AUSTRALIA 2012. Western Australia's Supertowns. Perth.
- GREY K, MOORE L, BURNE R, PIERSON B & BAULD J 1990. Lake Thetis, Western Australia: and example of Saline Lake Sedimentation dominated by Benthic Microbial Processes. *Marine and Freshwater Research* 41, 275–300.
- HALE J & BUTCHER R 2007. Ecological Character Description of the Peel-Yalgourup Ramsar Site, Report to the Department of Environment and Conservation and the Peel-Harvey Catchment Council, Perth, Western Australia.
- HORWITZ P, ROGAN R, HALSE S, DAVIS J & SOMMER B 2009. Wetland invertebrate richness and endemism on the Swan Coastal Plain, Western Australia. *Marine and Freshwater Research* 60, 1006–1020.
- JONES S M, PINDER A M, SIM L L & HALSE S A 2009. Evaluating the conservation significance of inundated basin wetlands within the Avon Natural Resource Management region: Stage Three Assessment Method. Prepared for the Avon Catchment Council by the Department of Environment and Conservation, Perth.
- KERN A M 1997. Hydrogeology of the coastal plain between Cervantes and Leeman, Perth Basin. Water and Rivers Commission, Perth.
- MAECHLER M 2013. Cluster Analysis Extended Rousseeuw *et al.* package for R.
- OXSANEN J, BLANCHETT F G, KINDT R, LEGENDRE P, MINCHIN P R, O'HARA R, SIMPSON G L, SOLYMOS P, STEVENS M H H & WAGNER H 2013. Vegan: Community Ecology Package, v2.0-8.
- PINDER A M, HALSE S A, McRAE J M & SHIEL R J 2004. Aquatic invertebrate assemblages of wetlands and rivers in the Wheatbelt region of Western Australia. *Records of the Western Australian Museum Supplement* 67, 7–37.
- PINDER A M & LEUNG A E 2010. Report on the August 2008 Sampling of the Aquatic Invertebrate Assemblages of Mound Springs of the Three Springs Area Threatened Ecological Community. Department of Environment and Conservation, Perth.
- PINDER A M & QUINLAN K 2011. Aquatic invertebrate communities of selected springs in the Jurien (Cervantes to Coolimba) region - Interim report to Department of Water. Department of Environment and Conservation, Perth.
- PINDER A M, QUINLAN K, CALE D J & LEUNG A E 2012. Aquatic invertebrates of the Hutt River and Hutt Lagoon catchments, Western Australia. *Journal of the Royal Society of Western Australia* 95, 29–51.
- PRIMER-E LTD 2008. Primer v6.1.11. Primer-E Ltd, Plymouth, UK.
- R DEVELOPMENT CORE TEAM 2013. R: A language and environment for statistical computing, v 3.0.0. R Foundation for Statistical Computing, Vienna, Austria.
- RSTUDIO 2013. RStudio: Integrated development environment for R (Version 0.97.449).
- RUTHERFORD J C, ROY V & JOHNSON S L 2005. The hydrogeology of groundwater dependent ecosystems in the Northern Perth Basin. Department of Environment, Perth.
- SEMIENIUK C A 1987. Wetlands of the Darling System – a geomorphic approach to habitat classification. *Journal of the Royal Society of West Australia* 69, 95–112.
- SEMIENIUK C A & Semeniuk V 2011. A comprehensive classification of inland wetlands of Western Australia using the geomorphic-hydromorphic approach. *Journal of the Royal Society of Western Australia* 94, 449–464.
- SUSAC R A C 2007. A Literature Review & Report of Karst Biodiversity, Palaeontology & Hydrology in the Northern Agricultural Region, Western Australia. Department of Environment and Conservation, Perth.
- SUSAC R, KERN S, PINDER A & DANIEL G 2009. Condition Report for a Significant Western Australian Wetland: Leeman Lagoon. Department of Environment and Conservation, Perth.
- TIMMS B V, PINDER A M & CAMPAGNA V S 2009. The biogeography and conservation status of the Australian endemic brine shrimp *Parartemia* (Crustacea, Anostraca, Parartemiidae). *Conservation Science Western Australia* 7, 413–427.
- WIITAKER D & CHRISTMAN M 2010. Clustsig: Significant Cluster Analysis Package for R, v 1.0.

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Higher taxonomy		Lowest level of identification	Site number																									
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Crustacea	Anostraca	Branchiopodidae	1							08	1			1														
		Sididae													1													
		Chydoridae														1				1	1							1
	Cladocera																			1	1							
																				1	1							
																				1	1							
																				1	1							
																				1	1							
																				1	1							
																				1	1							
Ostracoda	Daphniidae		1				1							1														
	Macrotrichidae																											
Copepoda	Cypridopsidae																											
Cyclopidae	Notodromadidae																											

[illegible]

Higher taxonomy	Lowest level of identification	Site number																									
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Diptera	<i>Megaporus solidus</i>													1					1								
	<i>Megaporus</i> sp.											1		1									1				
	<i>Rhantus suturalis</i>										1						1		1				1				1
	<i>Rhantus</i> sp.			1																		1					
	<i>Laucetes lanceolatus</i>													1				1					1				
	<i>Hyderodes</i> sp.			1	1						1																
	<i>Eretes australis</i>																										1
	<i>Spencerhydnus pulchellus</i>																		1								
	<i>Onycholigotus</i> sp.		1											1					1								
	Dytiscidae sp.						1																				
	Bidessini sp.			1							1			1					1		1						
	<i>Macrogyrus</i> sp.																		1								
	<i>Dinentus australis</i>																										
	<i>Berosus australis</i>																										1
	<i>Berosus approximans</i>																			1							
	<i>Berosus discolor</i>											1	1														1
	<i>Berosus maculibensis</i>			1																							
	<i>Berosus majusculus</i>																										
	<i>Berosus nutans</i>																										1
	<i>Berosus</i> sp.		1								1	1	1						1	1				1			1
	<i>Eutochrus elongatus</i>																										
	<i>Eutochrus maculiceps</i>																		1								
	<i>Limnuxenus zelandicus</i>																										
	<i>Limnuxenus</i> sp.			1																							
	<i>Paracygnus pygmaeus</i>		1	1							1								1								1
	<i>Hydrophilus</i> sp.																							1			
	Hydrophilidae			1																							
	Staphylinidae			1																							
	Scirtidae			1	1	1						1	1					1									1
	Curculionidae			1									1							1							1
	Tipulidae																										
	Tipulidae type C																										
	Tipulidae type E																										
	<i>Anopheles annulipes</i> s.l.				1										1										1		
	<i>Anopheles</i> sp.			1																							1
	<i>Aedes albopictus</i>				1																						1
	<i>Aedes camptorhynchus</i>		1			1																					
	<i>Aedes</i> sp.			1																							
	<i>Culex globocoxitus</i>																										
	<i>Culex australicus</i>			1																							
	<i>Culex</i> sp.				1																						1
	<i>Coquillettia linealis</i>																										
	<i>Bezzia</i> sp.																										
	<i>Bezzia</i> sp. 2																										
	<i>Culicoides</i> sp.																										
Ceratopogonidae		1																									

[illegible]

An opportunistic observation of Ghost Bat (*Macroderma gigas*) predation on six bird species within Karijini National Park

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ABSTRACT

This note describes an opportunistic observation of Ghost Bat (*Macroderma gigas*) predation of six native bird species inferred from prey remains discovered in a cave in Karijini National Park, Western Australia. A Ghost Bat was photographed grasping a Little Button-quail (*Turnix velox*) and the presence of accumulated prey remains on the cave floor revealed wings of six bird species that are assumed to have been preyed upon by this animal. A number of Sheath-tailed Bats (*Taphozous* spp.) were also roosting in the cave.

KEYWORDS: Ghost Bat (*Macroderma gigas*), Karijini National Park, Sheath-tailed bat (*Taphozous* spp.), prey, diet

INTRODUCTION

The Ghost Bat is the largest microchiropteran found in Australia. It has a patchy but widespread distribution north of the Tropic of Capricorn with a population recorded in the Pilbara, Western Australia (Richards *et al.* 2008). The species is an active predator of vertebrates and invertebrates that uses visual or audible searches to detect potential prey from a vantage point before pursuing and swooping. Prey items are caught while flying or are alternatively gleaned from vegetation and the ground. Prey is carried in flight to regularly-used roost sites inside caves, mines or under rock overhangs, where it is consumed. Uneaten remains accumulate underneath the roost site (Douglas 1967; Tidemann *et al.* 1985).

METHODS

During the course of an unrelated study (Johnston *et al.* 2013) within Karijini National Park, a cave was located in an area of low rocky hills to the south-east of Dinner Plate Hill. The entrance to the cave had an easterly aspect and was set back into the cliff line. We entered the cave at 1600 hrs on 31 July 2012 and found that it contained two chambers. The first measured approximately 4 m wide, 2 m high and 20 m long and constricted to a ~1 m diameter section before reopening into the second chamber of approximately 1 m wide, 1.5 m high and 5 m long and then terminated.

An accumulation of birds' wings, tails and plucked feathers was located in the first chamber. All wings were identified to species level based on plumage colour and pattern, and primary length. A count of left wings was made to determine the number of individual birds per species that those wings represented (right wings were not counted to avoid counting both wings of the same individual as two separate individuals).

RESULTS

We observed <20 Sheath-tailed Bats (*Taphozous* spp.) roosting in the first chamber and an individual Ghost Bat in the second chamber. As we entered this chamber, the Ghost Bat was observed grasping a bird carcass (Figure 1), which was then dropped as it exited the cave. The unconsumed bird was identified to be a Little Button Quail (*Turnix velox*) from which the head was missing, presumably removed by the bat (Figure 2). The head was located on the cave floor underneath where we had initially observed the ghost bat roosting.

The accumulation of bird wings, plucked feathers and bat scats, which formed two piles in close proximity suggested regular usage by bats (Figure 3). In total, 14 individual birds of six species were identified in the pile of prey remains (Table 1, Figure 4). The most common species was Budgerigar (*Melopsittacus undulatus*) (35% of wings) followed by White-winged Triller (*Lalage tricolor*) (21% of wings). Other species identified included Little Button Quail (*Turnix velox*), Australian Owlet-nightjar (*Aegotheles cristatus*), Masked Woodswallow (*Artamus personatus*) and a Honeyeater spp. (Meliphagidae) (Figure 4).

Both chambers in this cave were readily accessed by other wildlife species including predators such as feral cats (*Felis catus*) and dingo/wild dog (*Canis familiaris*). However given the arrangement and content of the two piles of bird remains, their proximity to large bat scats, and the presence of a Ghost Bat, there is little doubt that the remains are from the prey consumed by Ghost Bat.

DISCUSSION

Previous published reports describing the diet of Ghost Bats include invertebrate and vertebrate species (Douglas 1967; Tidemann *et al.* 1985). Schulz (1986) observed remains of bird species that can have a mass of up to 100–125g in the debris underneath Ghost Bat roost sites.



Figure 1. Ghost Bat holding prey (Little Button-quail) at a cave in Karijini National Park. (Photo: Neville Little and Les Bould).



Figure 2. Unconsumed prey (Little Button-quail) dropped by Ghost Bat. (Photo: Michael Johnston).



Figure 3. Accumulation of uneaten prey remains found in the first chamber (Photo: Neville Little).

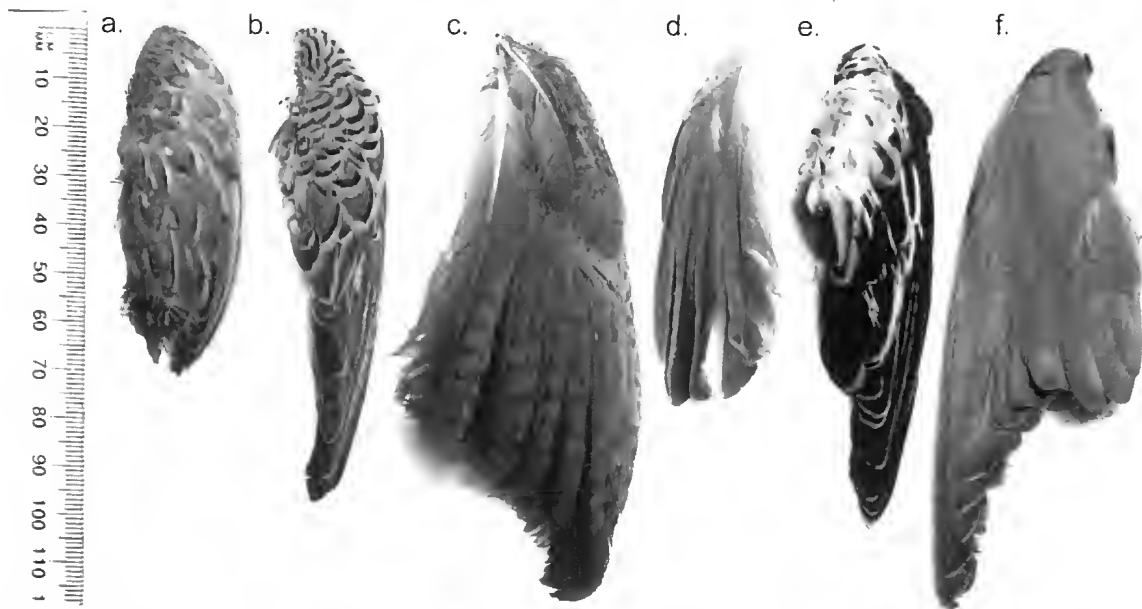


Figure 4. Bird wings collected from pile of accumulated prey remains and inferred to be prey of Ghost Bat. For identification see Table 1. (Photo: Ashley Herrod).

Table 1. Avian species, count of left wings and their proportion from total left wings, as identified from pile of prey remains. The letters refer to Fig. 4.

Species	Count of left wings	Percentage of total wings
b Budgerigar <i>Melopsittacus undulatus</i>	5	35
e White-winged Triller <i>Lalage tricolor</i>	3	21
a Little Button Quail <i>Turnix velox</i>	2	14
f Masked Woodswallow <i>Artamus personatus</i>	2	14
c Australian Owlet-nightjar <i>Aegotheles cristatus</i>	1	7
d Honeyeater spp. (Meliphagidae)	1	7

The prey species observed in this circumstance indicates a largest adult mass of 46.4 g (Australian Owlet-nightjar; mean weight of 41 unsexed adults; Higgins 1999). Predation of other bat species has been observed (Pettigrew *et al* 1986; Schulz 1986) but we did not detect any evidence to suggest that this Ghost Bat had preyed the Sheath-tailed Bats.

Our field observations were made six months after the passage of Cyclone Heidi during which 230 mm of rain fell over the site. The resultant response in vegetation growth and seeding supported abundant populations of granivorous birds such as Little Button Quail and Budgerigar (S. Berris, pers. comm.). The number of wings found on the cave floor in the main chamber indicate that multiple Budgerigars, White-winged Trillers and Little Button-quail had been consumed at that location. It is presumed that the first chamber was the preferred roosting location rather than the second chamber given that there was no accumulation of prey remains in the latter, other than the head of the quail. It is quite possible that we disturbed the Ghost Bat and it had retreated into the second chamber as we entered the cave.

The opportunistic detection of this Ghost Bat in Karijini National Park provides a snapshot of the species composition of its avian diet, and evidence of the continuing presence of this species within the Pilbara region.

ACKNOWLEDGEMENTS

Peter Menkhorst and Danny Rogers provided advice as to the identification of species represented by the wings recovered from the cave. Anonymous referees provided constructive comments that improved this manuscript. Kylie Eklom, Julie Quinn and Michael O'Donoghue assisted in conduct of the fieldwork.

REFERENCES

- DOUGLAS A M 1967. The Natural History of the Ghost Bat, *Macroderma gigas* (Microchiroptera, Megadermatidae), in Western Australia. *The Western Australian Naturalist* **10**, 125–138.
- HIGGINS P J (ed) 1999. *Handbook of Australian, New Zealand and Antarctic Birds. Volume 4: Parrots to Dollarbirds*. Oxford University Press, Melbourne.
- JOHNSTON M, O'DONOGHUE M, HOLDSWORTH M, ROBINSON S, HERROD A, EKLOM K, GIGLIOTTI F, BOULD L & LITTLE N 2013. *Field assessment of the Curiosity® bait for managing feral cats in the Pilbara*. Arthur Rylah Institute for Environmental Research Technical Report Series No. 245. Department of Sustainability and Environment, Heidelberg, Victoria.
- PETTIGREW J, BAKER G B, BAKER-GABB D, BAVERSTOCK G, COLES R, CONOLE L, CHURCHILL S, FITZGERBERT K, GUPPY A, HALL L, HELMAN P, NELSON J, PRIDDEL D, PULSFORD I, RICHARDS G, SCHULZ M & TIDEMANN C R 1986. The Australian Ghost Bat *Macroderma gigas*, at Pine Creek, Northern Territory. *Macroderma* **2**, 8–19.
- RICHARDS G C, HAND S, ARMSTRONG K N & HALL L S 2008. Ghost Bat *Macroderma gigas*. In: *The Mammals of Australia* (eds S Van Dyck and R Strahan). pp. 449–450.
- SCHULZ M 1986. Vertebrate prey of the Ghost Bat, *Macroderma gigas*, at Pine Creek, Northern Territory. *Macroderma* **2**, 59–62.
- TIDEMANN C R, PRIDDEL D M, NELSON J E & PETTIGREW J D 1985. Foraging behaviour of the Australian ghost bat, *Macroderma gigas* (Microchiroptera: Megadermatidae). *Australian Journal of Zoology* **33**, 705–713.

Geomorphology and Holocene Growth History of the Cockatoo Island Fringing Reefs, Kimberley Bioregion, Northwest Australia

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Located in the Northwest region of Australia, Kimberley coral reefs have a unique environment with macrotidal conditions, hard substrate geology, and ongoing subsidence compared to a microtidal and no subsidence setting environment of the Great Barrier Reef (GBR) in the east coast of Australia. Despite the fact that the Kimberley coral reefs are living in inhospitable environments, the coral species are far richer than those of the inner GBR and a little richer than those of the Pilbara to the south. However, the other invertebrate fauna of the Kimberley are relatively impoverished (Wilson 2013).

Subsidence since the Last Interglacial has provided accommodation for growth of a Holocene reef upon older reef substrate, both exposed in an excavation. The complexity of this region regarding the high biodiversity, high sediment input, geomorphic settings, and oceanographic conditions linked to an understanding of reef development still remains a gap in our knowledge and needs to be fully evaluated. Hence, reef mapping and transects was employed to obtain reef geomorphology and associated habitat, detailed stratigraphy, combined with palaeoecological and geochronological analysis, enabling an investigation into how these reefs were able to persist under extreme environmental conditions as well as respond to Holocene sea level change.

Contemporary reef communities and habitat were investigated on the reef flat using visual assessments and descriptions as a first stage to obtain information on modern reef communities and digital towed cameras were then deployed to aid recognition and interpretation. Reef transects were established to log the abandoned reef exposures in the Cockatoo mine-pit and four transects were selected evenly spaced along the workable exposure. At each site, a vertical 0.7 m wide transect from the base to the top was logged, sampled and photographed to obtain information including: (i) the ratio of coral clasts and matrix; (ii) sediment characteristics (visual assessment of sediment composition and the Udden-Wentworth nomenclature);

(iii) preliminary coral communities identification. Reef framework analysis and facies descriptions followed the terminology suggested by (Montaggioni, 2005), which highlights the growth of the dominant coral reef builders and environmental indicators. Position fixing was by DGPS tied to mine-site datum. Accelerator mass spectrometry (AMS) radiocarbon dating was used to establish a geochronologic record of reef accretion and recalibrated using CALIB Version 5.0.2 and calibration curve Marine04 (<http://calib.qub.ac.uk/marine>; accessed November 2012). All dated samples discussed in the text are calibrated in years Before Present (later written as cal y BP) with 68.2% (2 σ) probability range. Transect data from each site were replotted relative to the Australian Height Datum (AHD), which is -3.987 m of the Cockatoo mine grid.

The towed camera investigations confirmed that the reef geomorphology and associated habitat of the Cockatoo fringing reefs is divided into three zones, comprising: 1) reef flat which is colonised mostly by branching *Millepora* and *Porites Cylindrica*, 2) outer reef flat dominated by *Turbinaria* and branching *Porites*, and 3) forereef slope with branching *Acropora* dominant. The contemporary live corals are not very common in the measured Holocene sections, suggesting that the Holocene reef communities lack reef flat habitat. The Holocene reflects mostly subtidal growth whereas the present reef is largely intertidal or very shallow subtidal. The reef stratigraphy in the Cockatoo mine-pit shows whole Holocene reef exposure, overlain by mine-rock overburden and underlain by hematitic breccia and Pleistocene calcretised reef. The foundation is Proterozoic hematitic sandstone.

The reef facies throughout the section is dominated by branching coral framestone unit with muddy matrix, but we can also find a domal dominant coral horizon in some sections, which doesn't continue laterally. The Holocene reef thickness measured is about 8 to 13 m, and that is the minimum thickness because the upper contact of the reef section is obscured by mine-rock overburden. The longest section of the reef stratigraphy shows that the early reef initiation was at ~9ky BP at the depth of 18 m AHD and the reef cessation was at ~3ky BP at the depth of 5.5 m AHD. This indicates that the reefs here have grown about 13 m within 6k years as sea-level rose. The matrix throughout the section is dominated by unconsolidated grey-green mud with up to 49% carbonate content, indicating that the sediment is sourced from land/terrestrial processes.

* Extended abstract of a paper presented at the Royal Society of Western Australia Centenary Postgraduate Symposium 2014 held at The University of Western Australia on 3 October 2014.

The Holocene vertical reef and growth history of the Cockatoo fringing reefs shows that at the early stage of reef development, the reefs showed rapid growth with up to 11.4 mm/year at ~8ky BP and is classified as “keep-up” phase. The reef was interpreted establishing itself in a quite shallow environment, much light and high energy, so that the reefs grew keeping-up the sea-level. Following that, the sea-level overtook and the reefs lagged behind due to water depth, less light and low energy, thus the reefs experienced slowing growth with maximum growth rate only 2 mm/y which is classified as “catch-up” phase. At the end, when the reef nearly reached sea level, with increasing energy, much light, and shallow water, the reefs changed back to a “keep-up” phase with maximum 27 mm/year accretion rates.

As a comparison, Cockatoo growth history records keep-up initially with the Abrolhos curve in SW Australia with microtidal conditions and no-subsidence, but then lags behind, whilst Abrolhos reefs grew vertically to near sea-level until the highstand was recorded (Collins *et al.*, 1996). Scott reef of the oceanic shoals which represent macrotidal conditions and high

subsidence rates since LIG, allows comparison of subsidence rates averaging 0.1 mm/y for Cockatoo and up to 0.45 mm/y for Scott reef (Collins *et al.*, 2011). Finally, with respect to the reef in GBR which has a muddy reef environment as does Cockatoo (Perry *et al.*, 2012), the reef foundation in GBR is shallower with much shorter history, very small (thinner) growth, and microtidal conditions.

This investigation is the first information on Holocene reef growth for the inshore Kimberley Bioregion and this also recorded the coastal subsidence of LIG substrate reef at Cockatoo Island with 0.1 mm/y rate. Comparison with turbid reefs of the inner GBR shows broad similarities in terms of mud-dominated matrix, sediment-tolerant coral, high coral cover, and similar growth rates with the exception of palaeoecological and contemporary reef communities which are similar in GBR but different at Cockatoo. The Cockatoo reef community has also evidenced adaptation to high sediment loads and frequent exposure. The study provides the first Holocene reef growth history for an inshore Kimberley reef within a biodiversity “hotspot”.

Subbottom profiling and growth patterns of Kimberley coral reefs, North West Australia *

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The Kimberley region is located in the north western continental margin of Australia and is characterised by unique and complex geology and geomorphology that spans almost 2 billion years. The modern marine environment, considered as one of the world's greatest biodiversity hotspots, is significantly influenced by the interaction of long term processes, such as pre-existing rock foundation (Proterozoic Sandstone), Quaternary subsidence and Holocene/Pleistocene sea level fluctuations, and short term factors, like macrotidal range systems (up to 11 m), tropical monsoonal climate, high turbidity (related to terrigenous inputs from active rivers) and warm ocean temperatures.

Due to the remoteness, vastness and complexity of the Kimberley region, the marine and coastal environment is still poorly investigated. In 2011, the Western Australia State Government funded through the Western Australia Marine Science Institution (WAMSI) an extensive marine research program, in order to fill the present gap in the scientific knowledge and support the management of the coastal waters in the southern Kimberley. This research, as part of the plan (project 1.3.1, WAMSI Kimberley Marine Research Program), aims to study the morphostratigraphic evolution and distribution of various southern Kimberley reef settings, and determine their internal reef architecture and interaction with the environmental elements.

294 km of high-resolution shallow imaging data represent the first detailed seismic study in the region. Acoustic datasets were collected with an AA201 boomer SBP and interfaced with a dual frequency Differential Global Positioning System (DGPS) in order to obtain an accurate position (decimetric accuracy).

The survey sites were predetermined and targeted in order to evaluate most of the reef types represented in a preliminary classification scheme developed for the southern Kimberley coral reefs. The classification comprises a hierarchical subdivision of the reefs. In the first order the reefs are divided into high intertidal (elevated reefs whose surface is several metres above Mean Low Water Spring tides), intertidal and subtidal on the basis of their vertical position in relation to the sea level. The second rank is based on reef geomorphology

and comprises fringing reefs, planar reefs, patch reefs and shoals. The third level further subdivides each reef type, accordingly to their configuration in relation to the shoreline and architecture. In this level, five main types of fringing reef are described (bay head, interisland, circum island, headland and narrow beach base) and two for each other reef (planar reefs: sand lagoon or coralgall; patch reefs: irregular or unbroken margins; shoal: sand or coral).

Solihuddin *et al.* (2015) examined in detail the stratigraphy and geochronology of Cockatoo Island and this research refers to their results as starting point to calibrate the seismic data. Within the Buccaneer Archipelago, besides the Cockatoo fringing reef, the neighbouring fringing reefs of Irvine and Bathurst islands were also surveyed to verify the consistency of the calibration of the internal reflectors and acoustic reflection characteristics. Montgomery was selected as special type of planar reef. Turtle, Sunday and Tallon reefs were targeted because of their variety of fringing reef types. In the offshore (mid shelf ramp) southern Kimberley region, the planar reefs around the Adele complex were surveyed and correlated with the results of a well drilled in 1982, in the northern tip of Adele Island.

During the post processing and interpretation of the acoustic datasets, significant seismic reflectors were considered on the basis of their relative position, acoustic reflection and architectural characters and identified through the correlation with the Cockatoo mine pit sections.

Within the inner shelf reefs, the deepest acoustic horizon depicted in the seismic profiles is reflector RF. It forms deep valley-like depressions and ridges and caps a Proterozoic rock foundation which is the acoustic basement of the inshore reefs. Between RF reflector and the seafloor, reflector R1 is present and represents the top of the Pleistocene calcretised reef unit, related to the last interglacial (LIG, MIS 5e, ~ 125 ky BP) sea level highstand. The reflector R1 displays a similar trend to the modern reef morphology (seafloor), with a quasi-horizontal reef flat and a steep forereef. The seismic unit bounded by the seafloor and reflector R1 represents the Holocene reef/sediment buildup, characterised by a series of internal discontinuous, subparallel reflectors (H1, H2 and H3) which could be interpreted as hiatuses or temporary pauses in reef growth. The thickness of the Holocene and the LIG reefs vary in relation to the depth of the Proterozoic bedrock. In the Buccaneer Archipelago, Turtle and Montgomery reefs, the rock foundation lies at

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30 – 40 m below sea level and is relatively flat. The LIG sequence is mainly present below the Holocene reef, where it is approximately 10 – 15 m thick. The Holocene reef buildup averages around 15 m, but it reaches 22-25 m of thickness immediately under the platform of Montgomery and Cockatoo reefs. Under Sunday and Tallon reefs, the pre-existing Proterozoic topography rises from below 30 m to 10 – 15 m below the seafloor, significantly reducing the reef development and resulting in Last Interglacial and the Holocene reefs being relatively thin (about 7 m).

In the mid shelf reefs, the Proterozoic basement is at 798 m and, within equipment limitations, seismic profiles of the Adele platform identified two further reflectors. The deepest acoustic horizon is reflector R3, at 65 m below the sea level, capping an older reef unit, tentatively considered to be MIS 9 (about 300 ky BP). At 35 – 41 m below the sea level, a further reflector (R2) can

be detected. As would be predicted by the Marine Isotope Curve, reflector R2 could represent the top of MIS 7 (~ 190 ky BP) carbonate unit, about 25 m thick. As found in the inner shelf reefs, reflector R1 can be observed also in the northern portion of Adele, separating the LIG reef (about 3 – 10 m thick) and the Holocene package (usually 20 – 30 m thick).

These new datasets provided a better understanding of Quaternary reef growth. Some of the key interacting factors in coral reef classification and growth include morphology, setting, physical processes, antecedent topography and sea level change. By developing an understanding of seismostratigraphic events, it has been possible to document the subsurface evolution and growth history of diverse reef systems for a range of reef types mapped in the southern Kimberley, at the scale of multiple reef building stages correlated to the Marine Isotope Curve.

Seasonality and distributions of macro-algae *Sargassum* beds at Point Peron, Shoalwater Islands Marine Park, Western Australia *

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Sargassum C. Agardh is one of the most diverse genera of the marine macro-algae, is distributed worldwide, and is mainly dominant in tropical and sub-tropical shallow waters. There are about 46 *Sargassum* species found along the Western Australia (WA) coast (Herbarium 2013), with the large majority of studies on WA's macro-algae focusing on taxonomic and molecular works (e.g. Kendrick & Walker 1994; Goldberg & Huisman 2004; Dixon *et al.* 2012; Kendrick *et al.* 2012). A number of other studies have focused on seaweed physiology including green macroalgae (De Clerck *et al.* 2008) and red macro-algae (Huisman *et al.* 2009; Muñoz & Fotedar 2011). Up to date, there are a limited number of studies on seasonal variation on *Sargassum* communities that have been undertaken along the subtropical/temperate coastal zone of WA (Kendrick 1993; Kendrick & Walker 1994).

This study was carried out to investigate the seasonality of water qualities, canopy cover, thallus length and distribution of *Sargassum* beds around Point Peron, Shoalwater Islands Marine Park, WA. The aim was to improve our understanding of the seasonal abundance and distribution of *Sargassum* and the effects of water quality parameters on their biomass. Here we measured the seasonal variation in physico-chemical water parameters alongside changes in mean thallus length, density and total biomass of *Sargassum* and determined how this impacts the broader spatial distribution of *Sargassum* beds using *in-situ* observations and remote sensing methods.

The data on canopy cover, thallus length and distribution patterns were collected every three months from 2012 to 2014 at four different reef zones along monitored transects. Sampling was carried out by either scuba or free diving techniques. Along these monitoring transects, a total of three sites were randomly selected within the lagoon, back reef, reef crest and fore reef zones. Measurements of fresh biomass, cover percentage, and thallus length were made by deploying 0.25 m² quadrats (0.5 x 0.5 metre), with a total of 12 tagged quadrat sites established. The tagged quadrats' locations were recorded with a hand held GPS (Garmin Etrex 10) for storage and easy re-navigating during the following sampling season. *Sargassum* spp. within each quadrat were collected, stored in labelled plastic bags and carried to Curtin Aquatic Research Laboratory, Curtin

University, WA for further analysis and experiments. Meteorological data such as maximum, mean and minimum air temperature, monthly rainfall and monthly solar exposure for each season were acquired from the Garden Island HSF weather station, two kilometres north of Point Peron, Bureau of Meteorology, Australian Government (<http://www.bom.gov.au/climate/data/>). Euphotic depth, Coloured Dissolved Organic Matter (CDOM), Photosynthetically Available Radiation (PAR), Sea surface temperatures (SSTs), Sea level pressure, and Chlorophyll-a concentration (Chl-a) in the study area were extracted from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data (Acker & Leptoukh 2007). Dissolved oxygen, salinity, pH, conductivity of seawater were *in-situ* measured from the field (YSI®55, Perth Scientific). Five seawater samples were collected for analysis of nutrients concentration including nitrate, nitrite, ammonia, and phosphate for each sampling season. High spatial resolution satellite images WorldView-2 with 2 m spatial resolution was acquired on February 7th 2013 (austral summer) and, along with the period of highest biomass of *Sargassum* beds, was used to estimate the spatial distribution pattern of *Sargassum*.

The results showed that the *Sargassum* beds in Point Peron showed remarkable seasonal changes in canopy cover and thallus length. There was a significant difference in *Sargassum* canopy cover between seasons. However, there were no significant differences between the reef zones. Results also show that the *Sargassum* spp. community demonstrated a seasonal variation pattern of coverage and mean thallus length which is significantly influenced by the nutrient concentrations (PO₄³⁻), sun radiation, collecting zone, and collecting season ($P < 0.05$). There are many different physical, chemical and biological parameters that affect the *Sargassum* community. They might contribute to optimum conditions for *Sargassum* growth as well as limitation factors such as the effect of water temperature, radiation and rainfall on *Sargassum* canopy cover, thallus length and distribution; the interaction of the *Sargassum* communities on water quality and vice versa; the effect of geographical zone (reef zones) on water quality; the variation of water temperature, radiation and rainfall at different geographical zones (study sites); the effect of air temperature, radiation and rainfall factors on water qualities and the season's conditions; and the seasons also driving changing water qualities and influencing *Sargassum* growth. In this study, we were evaluating the effect of environment parameters on *Sargassum* cover; the effect of sea surface temperature on *Sargassum* community and the relationship between nutrient

* Extended abstract of a paper presented at the Royal Society of Western Australia Centenary Postgraduate Symposium 2014 held at The University of Western Australia on 3 October 2014.

concentration and *Sargassum* thallus length. However, the understanding of how *Sargassum* communities affect water quality and differences in water qualities at different geographical areas has not been examined in this study yet.

In summary, the present study presents first hand baseline information on the effect of seasons on canopy cover and mean length thallus of *Sargassum* species at the different reef zones. Results show that the *Sargassum* spp. community demonstrated a seasonal variation pattern in coverage and mean thallus length which is significantly influenced by the nutrient concentrations (PO_4^{3-}), sun radiation, collecting zone, and collecting season ($P < 0.05$). This study demonstrates primary and novel information on *Sargassum* beds' structure of Point Peron by using a combination of *in-situ* and satellite remote sensing observations. These detailed data might provide necessary information for coastal marine management and conservation as well as sustainable utilisation of this renewable marine resource. The methods can also be applied as a bio-monitoring programme for *Sargassum* beds along the WA coast and in other potential regions.

ACKNOWLEDGEMENTS

The authors sincerely thank the Department of Parks and Wildlife, WA for authorization to collect seaweed in Point Peron, Shoalwater Islands Marine Park. Many thanks to Mr. Simon Longbottom and Mrs Anne Barnes at Curtin Aquatic Research Laboratory for their efficient assistance in laboratory consumables and fieldwork equipment. The authors also thank Ngoc Nguyen B. for assistance with the field works at different times throughout the project.

REFERENCES

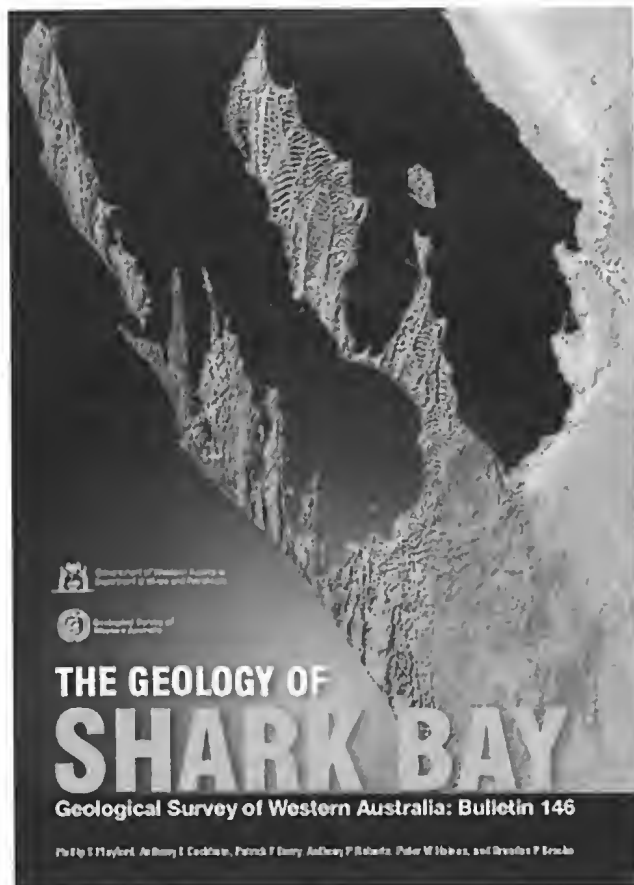
- DE CLERCK O, VERBRUGGEN H, HUISMAN J M, FAYE E J, LELIAERT F, SCHILS T & COPPEJANS E 2008. Systematics and biogeography of the genus *Pseudocodium* (Bryopsidales, Chlorophyta), including the description of *P. natalense* sp. nov. from South Africa. *Phycologia* 47, 225–235.
- DIXON R R M, HUISMAN J M, BUCHANAN J, GURGEL C F D & SPENCER P 2012. A morphological and molecular study of Austral *Sargassum* (Fucales, Phaeophyceae) supports the recognition of *Phyllotricha* at genus level, with further additions to the genus *Sargassopsis*. *Journal of Phycology* 48, 1119–1129.
- GOLDBERG N A & HUISMAN J M 2004. *Sargassum kendrickii* (Fucales, Phaeophyceae), a new species of subgenus *Phyllotricha* from southern Australia. *Botanica Marina* 47(5), 424–430.
- HUISMAN J M, PHILLIPS J C & FRESHWATER D W 2009. Rediscovery of *Gelidiella ramellosa* (Katzing) Feldmann et Hamel (Gelidiales: Rhodophyta) from near the type locality in Western Australia. *Cryptogamie Algologie* 30, 3–16.
- KENDRICK A, HUISMAN J & RULE M 2012. Life on the edge: intertidal reefs of the Marmion and Shoalwater Islands marine parks. *Landscape* 27, 52–58.
- KENDRICK G A & WALKER D I 1994. Role of recruitment in structuring beds of *Sargassum* spp. (Phaeophyta) at Rottnest Island, Western Australia. *Journal of Phycology* 30, 200–208.
- MUÑOZ J & FOTEDAR R 2011. Seasonal variations of agar extracted from different life stages of *Gracilaria cliftonii* (Gracilariaceae, Rhodophyta) from Western Australia. *African Journal of Marine Science* 33, 59–65.

Book Review

The Geology of Shark Bay

P E Playford, A E Cockbain, F F Berry, A P Roberts, P W Haines, and B P Brooke (2014).

The Geology of Shark Bay. Geological Survey of Western Australia: Bulletin 146. \$70; a pdf file can be downloaded from the WA Department of Mines & Petroleum website, gratis.



For many coming from an earth science background, 'Shark Bay' was indelibly imprinted on their minds during the beginning stages of an undergraduate career. So, a first visit to Shark Bay has been a scientific milestone for many – including this reviewer. The experience of actually seeing living stromatolites, algal structures that already populated the globe in the Precambrian, leaves a lasting imprint. The fascination of stromatolites and an awareness of their setting in Shark Bay goes well beyond the immediate scientific community, as evidenced by the Attenborough series and volume. But what has been missing has been an informed summary overview that captures the

importance and uniqueness of the setting. The volume by Playford and co-authors provides just this, and in Playford's case, summarises work that extends over more than fifty years.

The monograph opens with an outline of the history of the region, drawing on some fascinating illustrations. The reader is then guided through an outline of the oceanography, geomorphology and geology of the region. Themes such as sealevel change, tsunamis, recognition of past climate events and tectonics places the regional focus of the work into a wider geological-environmental context. Numerous radiocarbon and luminescence dates are used to provide the chronological context of events and successions. Of considerable significance to the Quaternary geologist, is the age model, albeit tentative, that is presented for the type section of the Tamala Limestone. In discussing their Shark Bay findings, the authors draw on relevant information from related areas (e.g. Rottnest Island and Cape Range), and this is an effective way of drawing out their wider significance and relevance.

The Hamelin Coquina and stromatolites are highlighted and given, rightly so, a great deal of attention. The Holocene beach ridge successions represented by the Hamelin Coquina, provide both useful analogues for coquina reservoirs in the geological record and are supposed to act as guides to the Holocene tropical cyclone record. So, that the details presented by the authors, coupled with other work, have far-reaching implications. The discussion of stromatolites deals with the details of distribution, classification, morphology and growth rates but as part of the introduction provides an outline of the history of investigation – and the role that different investigators have played since stromatolites were first recognized in Shark Bay. Combined, this provides an interesting and useful overview of the topic for the non-specialist.

As with all work, the authors have provided the opportunity for questions to be raised and criticisms advanced – that is the way science works. Be that as it may, the authors have laid the foundation for more focused future studies and have provided an outstanding regional monograph. The number of plates/illustrations is staggering (436) – there are few authors who would be allowed such latitude! The volume is very readable, enjoyable, highly recommended and deserves a wide readership.

K-H Wyrwoll

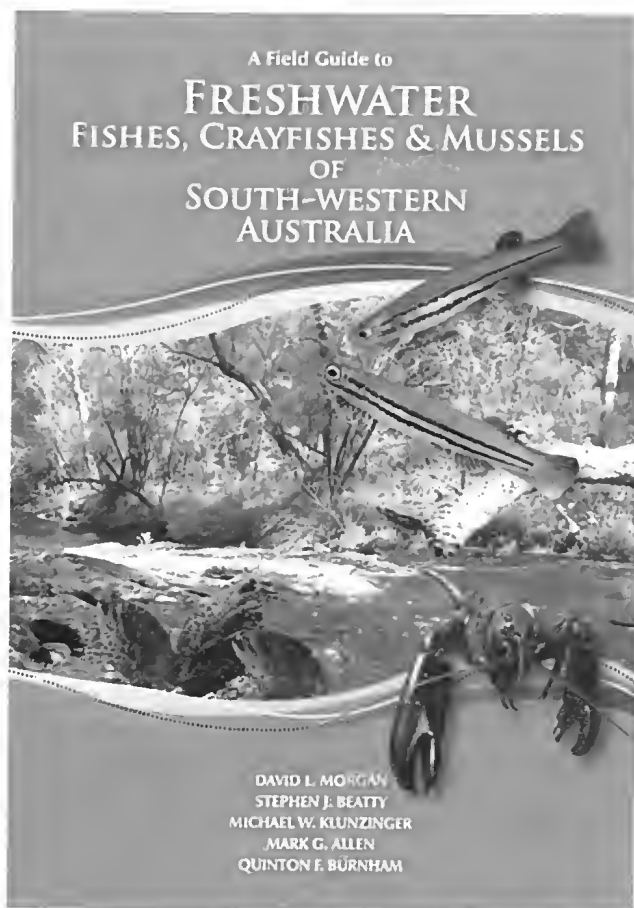
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Book Review

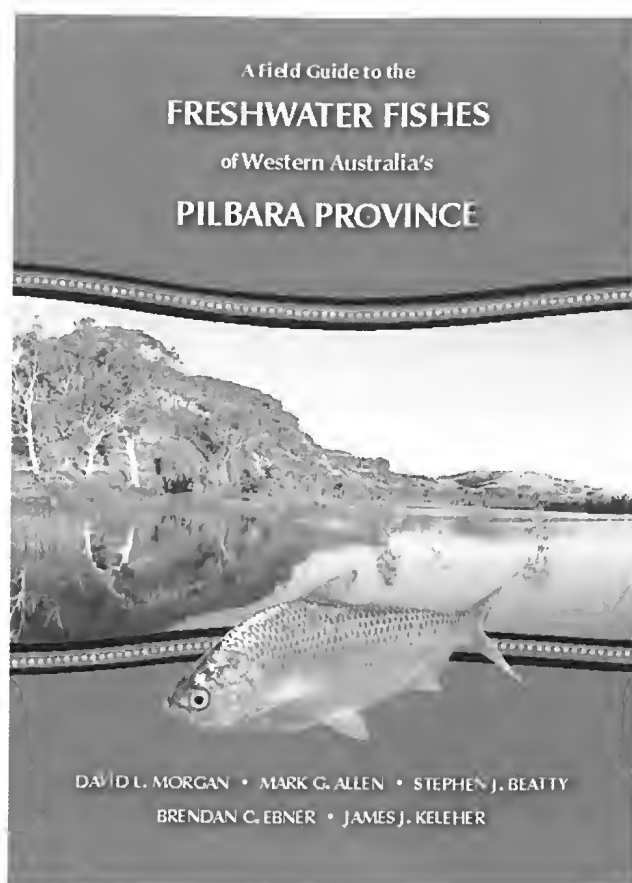
A Field Guide to Freshwater Fishes, Crayfishes & Mussels of South-western Australia,

A Field Guide to the Freshwater Fishes of Western Australia's Pilbara Province

D L Morgan, S J Beatty, M J Klunzinger, M G Allen, & Q F Burnham; *A Field Guide to Freshwater Fishes, Crayfishes & Mussels of South-western Australia* (2011): gratis.



D L Morgan, M G Allen, S J Beatty, B C Ebner & J J Keller, *A Field Guide to the Freshwater Fishes of Western Australia's Pilbara Province* (2014). Murdoch University Fish Group. \$10.



Well-illustrated field guides to some biological groups (such as birds or flowering plants) are available for almost every part of the world. Those for freshwater fish and other freshwater creatures are less easily found. There is nothing comparable to these two guides for two important bioregions of Western Australia. These handy booklets are illustrated by excellent photographs of each organism: these are supplemented by well-chosen habitat photos. Each species is described in sufficient detail for it to be identified and brief accounts are given on its biology. Notes on distribution are accompanied by sketch-maps. Useful keys are included and detailed

references are given. Each booklet has a glossary. The conservation status of each species is given: both booklets emphasise management and conservation aspects. For example, the precarious position of the extraordinary fauna of blind cave-dwelling fishes in the North West Cape Sub-Province is discussed in the Pilbara booklet, and the ecological dangers posed by the unauthorised introduction of non-native species is stressed in both publications. The booklets are conveniently sized for pocket or back-pack.

P H Armstrong

School of Earth and Environment, University of Western Australia.

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